Author:
Staniewicz, Agata M

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Acoustic communication of rare and threatened crocodilians and its use for population monitoring

Acoustic communication of rare and threatened crocodilians and its use for population monitoring

By

AGATA MARIA STANIEWICZ

School of Biological Sciences
UNIVERSITY OF BRISTOL

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Abstract

Freshwater animal populations can be more vulnerable to human impact than those in terrestrial and marine ecosystems, but may receive less conservation investment, often due to limited availability of information. In this thesis I explore strategies for the conservation monitoring of crocodilians, an iconic group of apex predators that play a key role in tropical freshwater ecosystem regulation, but are unfortunately vulnerable to human activities. Population assessments, crucial in developing conservation programs, require robust methodologies that take advantage of our knowledge of organismal biology and ecology. Traditional crocodile survey techniques that rely on spotlight or aerial counts are well established for the more conspicuous species, but can provide limited information when applied to species that are shy or difficult to access. These hard-to-survey species are also often the ones that are most vulnerable to habitat modification, and are consequently of greater conservation concern. Crocodiles are the most vocal of reptiles, which opens up the potential for novel methods of surveying. Here I provide baseline information on general ecology and acoustic communication in three threatened crocodilian genera in Africa and Southeast Asia—*Mecistops*, *Osteolaemus*, and *Tomistoma*—and then go on to test how the crocodile vocalisations can be exploited in a monitoring and survey context. I find that: (i) sympatric African crocodiles are highly partitioned in their habitat preferences, and so monitoring methods need to be tailored to individual species ecology, even when species are found in close proximity; (ii) West African slender-snouted crocodiles, *Mecistops cataphractus*, of all size classes produce distress calls and will respond to pre-recorded calls of their own species, but while the calls produced by small individuals attract conspecifics of all size classes, calls emitted by adults tend to repel them; (iii) spotlight surveys incorporating playback of *Mecistops* distress calls show greater detection rates compared to spotlight-only surveys; (iv) spotlight-only surveys detect a greater number of *Mecistops* than passive acoustic monitoring; (v) adult Central African dwarf crocodiles, *Osteolaemus tetraspis*, produce four distinct vocalisation types previously unreported in crocodylids, and are readily detected during passive acoustic monitoring; (vi) adult Sunda gharials, *Tomistoma schlegelii*, produce a range of previously-unreported underwater acoustic signals, but these appear restricted only to direct mating activities, therefore limiting utility of acoustic monitoring for their population assessment. This research provides an insight into the diversity of crocodilian acoustic repertoires, offers potential for acoustic-based survey methodologies in conservation, and opens up exciting new directions in reptile behavioural ecology.

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AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such below. Any views expressed in the dissertation are those of the author.

- Recordings of dwarf crocodile calls at Bristol Zoo were made by the University of Bristol project students (Monica Gojral and Molly Hackett). Recordings of wild dwarf crocodiles in Gabon were made by The Elephant Listening Project (Chapter 4).
- Data on Gabon playback were collected by Matt Shirley (Chapter 6).

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List of acronyms and symbols

Δ	Delta
χ	Chi
aff.	Affinis (Latin)
AIC	Akaike Information Criterion
df	Degrees of freedom
EO	Eyeshine only
HOTA	Head-oblique-tail-arched
SAVs	Sub-audible vibrations
SD	Standard deviation
SE	Standard error
SFM	Spectral flatness measure

CHAPTER 1

INTRODUCTION

1.1 Biodiversity monitoring and conservation of freshwater ecosystems

Freshwaters such as rivers, lakes, wetlands and reservoirs occupy only 2.3% of the Earth's surface, but are among the richest and most productive ecosystems, estimated to host at least 9.5% of known animal species (Reid et al., 2019). They provide a range of important ecosystem functions, including water storage and purification, flood regulation, storm protection, as well as services crucial to humans such as water supply, fisheries, transport and support for agriculture (Strayer and Dudgeon, 2010; The Ramsar Convention Secretariat, 2016).

However, freshwater ecosystems are currently also among the most threatened (Dudgeon et al., 2006; Reid et al., 2019). According to the World Wildlife Fund for Nature's Living Planet Index (WWF, 2016), animal populations monitored in freshwater habitats are declining at a faster rate than those in marine and terrestrial ecosystems, with the largest declines in the tropics, particularly among reptiles, amphibians and fishes (WWF, 2018). The biggest dangers are habitat loss and modification, overexploitation of resources, invasive species, pollution and climate change (WWF, 2016), but new emerging threats, including microplastics, light and noise pollution, algal blooms and infectious diseases will likely lead to further extinctions (Reid et al., 2019).

Unfortunately, tropical freshwater conservation attracts relatively little public, political and scientific attention (Cooke et al., 2016), with aquatic freshwater species being the focus of fewer than 16% of recent conservation studies carried out in Africa and Southeast Asia (Di Marco et al., 2017; Reid et al., 2019). As the ranges of 84% of threatened freshwater megafauna occur outside protected areas (Carrizo et al., 2017), efficient, cost-effective monitoring is crucial for informed

conservation management (Danielsen et al., 2005).

1.2 Conservation of crocodilians

Reptiles are the most threatened of the freshwater taxa (Collen et al., 2014), with crocodilians being the largest in body size (Somaweera et al., 2019). As apex predators, they provide a number of ecological functions, from the direct effects on prey species and food webs, through facilitating nutrient flow and linkage across different systems, to acting as habitat engineers by building nests and water refuges (Kushlan, 1974; Mazzotti et al., 2009; Nifong, 2018).

1.2.1 Species diversity, distribution and habitat ecology

Crocodilians are found in tropical and subtropical regions of Africa, Americas, Asia and Australia. There are at least 28 extant species (Grigg and Kirshner, 2015; Shirley et al., 2018; Murray et al., 2019), divided into three families and nine genera: Gavialidae (*Gavialis* and *Tomistoma*), Alligatoridae (*Alligator*, *Caiman*, *Melanosuchus* and *Paleosuchus*) and Crocodylidae (*Crocodylus*, *Mecistops* and *Osteolaemus*) (Martin, 2008; Grigg and Kirshner, 2015) (Fig. 1.1). All species are relatively late-maturing and long-lived (Grigg and Kirshner, 2015). While hatchlings and juveniles are vulnerable to a range of aquatic, terrestrial and avian predators (Somaweera et al., 2013), adult crocodilians have few natural predators, and thus high survivorship (Grigg and Kirshner, 2015).

All crocodilians are semi-aquatic, requiring water to mate, and are found in a diversity of freshwater habitats, including rivers, streams, wetlands, lakes, swamps, marshes, billabongs, and lagoons (Martin, 2008), with some species able to adapt to saltwater conditions (Martin, 2008; Grigg and Kirshner, 2015). While several species, such as *Crocodylus niloticus*, *Crocodylus porosus*, *Caiman crocodilus* or *Alligator mississippiensis* can be considered habitat generalists, with a broad distribution, many crocodilians are restricted in their range, with small, fragmented populations in the remaining suitable habitats (Martin, 2008).

Habitat preferences vary between species, with some, such as *Gavialis gangeticus*, or *Tomistoma schlegelii* preferring more continuous aquatic habitat, and others, such as *Crocodylus rhombifer*, *Crocodylus johnstoni* or *Caiman yacare* moving on land between smaller, isolated water bodies, particularly during the dry season (Campos et al., 2003; Trutnau and Sommerlad, 2006; Grigg and Kirshner, 2015). Nesting ecology can affect habitat preferences as well. While the majority of crocodilians build mound nests—either from organic matter assembled on floating vegetation (eg. *C. porosus*, *Crocodylus siamensis*; Magnusson et al., 1980; Staniewicz et al., 2018), or on land, often at the base of a large tree (eg. *Mecistops* spp., *T. schlegelii*; Bezuijen et al., 2001; Shirley et al., 2018)—seven species, including *Crocodylus johnstoni*, *C. niloticus*, and *G. gangeticus* nest in holes excavated on beached or river banks (Brazaitis and Watanabe, 2011).

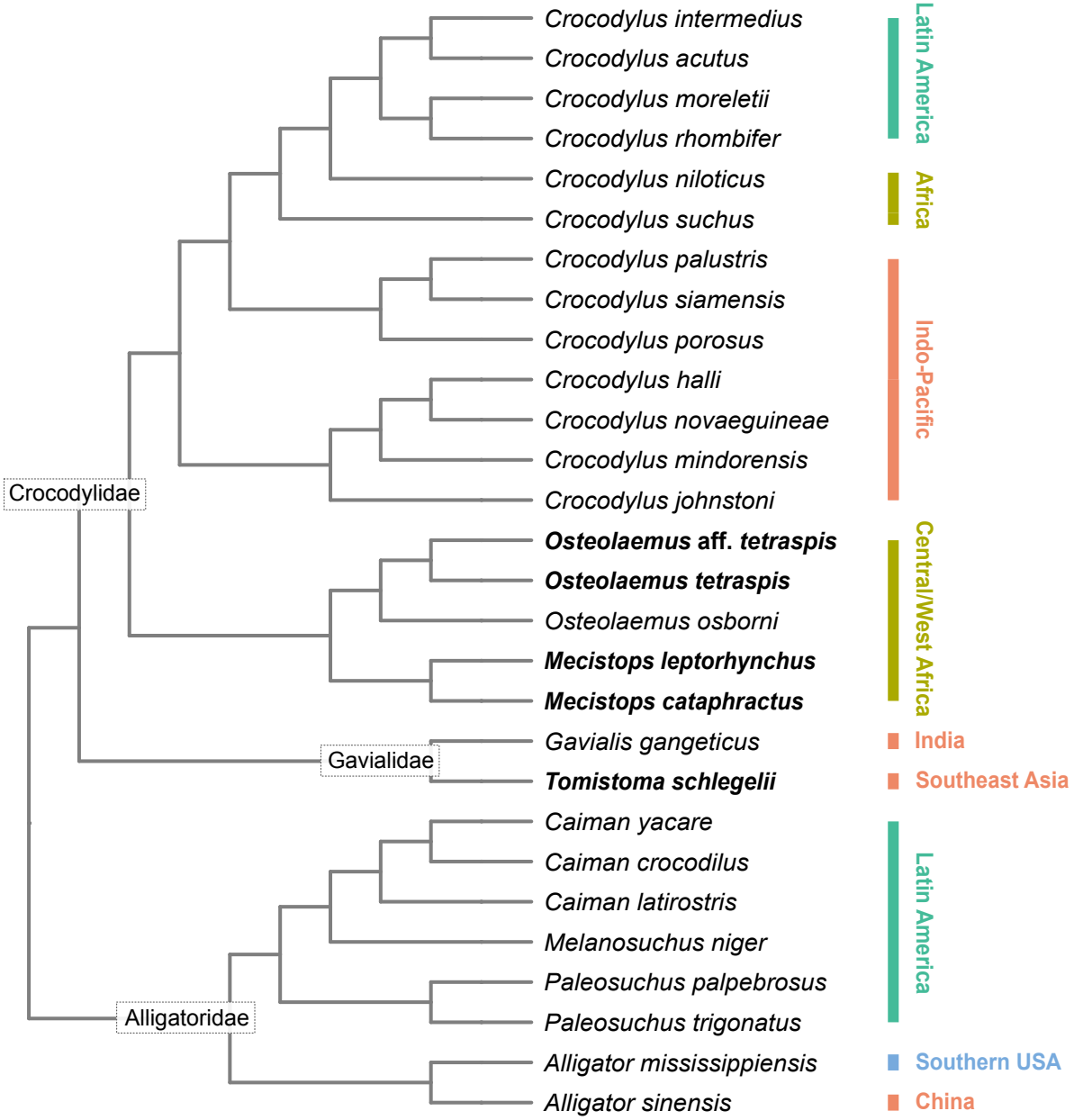

FIGURE 1.1. A cladogram representing the phylogenetic relationship and geographic distribution of the extant crocodilians (Oaks, 2011; Lee and Yates, 2018; Murray et al., 2019), redrawn with modification from Grigg and Kirshner (2015), incorporating the divergent *Osteolaemus* spp. (Eaton et al., 2009), the recently confirmed *Mecistops leptorhynchus* (Shirley et al., 2018), and *Crocodylus halli* (Murray et al., 2019). Species which are the focus of this thesis are highlighted in bold.

1.2.2 Behaviour and communication

Although, as ambush predators many crocodilians appear to lead largely solitary lifestyles, social interactions with conspecifics occur throughout all life stages (Garrick and Lang, 1977; Thorbjarnarson and Hernández, 1993; Grigg and Kirshner, 2015). Crocodilians use visual, acoustic and olfactory signals for communication (Grigg and Kirshner, 2015). While visual and olfactory cues such as body posture changes or pheromone releases are observed primarily in adults during courtship and territory defence (Vliet, 1989; Grigg and Kirshner, 2015), acoustic signals are used at all life stages (Vergne et al., 2009).

The young produce calls inside the egg to synchronise hatching and solicit parental help (Vergne and Mathevon, 2008) and to maintain crèche cohesion as hatchlings through contact calls (Britton, 2001; Vergne et al., 2009). Hatchlings, juveniles and occasionally adults signal threats and solicit help by emitting distress calls (Vergne et al., 2009, also see Chapter 5.1), while most adult vocalisations are heard during courtship and territory defence (Vergne et al., 2009; Grigg and Kirshner, 2015, also see Chapter 4.1). The behaviour is conserved between and within species, in both captive and wild animals (Setner, 2008), but the frequency of use of acoustic signals by adults varies between species and between habitats, particularly for long-distance communication (Dinets, 2011). Dinets (2011) found crocodilians living in fragmented aquatic habitats to use predominately vocal signals that travel through the air, such as roars or bellows, while the species found in continuous aquatic habitats used acoustic signals that dissipate through water better, such as sharp head slaps combined with low-frequency pulses.

Social behaviour and communication are also affected by population density. For example, in *A. mississippiensis*, *C. niloticus* or *C. yacare*, which can seasonally aggregate in large numbers over a limited area (Campos et al., 2003; Grigg and Kirshner, 2015), as well as in dense groups of captive *C. porosus* on farms, frequent visual dominance displays are commonly observed (Trutnau and Sommerlad, 2006). Additionally, in *Alligator* spp., adults, particularly males, attract mates by forming bellowing choruses during the breeding season, similar to lekking bird species (Vliet, 1989; Wang et al., 2007). Alligators are considered to be the most vocal genus (Wang et al., 2007; Grigg and Kirshner, 2015), and the classification of adult vocal and non-vocal acoustic signals has been developed primarily though studies on *A. mississippiensis* (Garrick et al., 1978; Wang et al., 2007; Dinets, 2013c; Reber et al., 2015). Although acoustic communication in *C. niloticus* and few *Caiman* spp., particularly between parents and offspring, has been a subject of several studies (Vergne et al., 2007, 2011, 2012; Chabert et al., 2015), relatively little is known about the social behaviour and communication in the species that are rare and threatened.

1.2.3 Conservation and monitoring

Of the 23 crocodilian species for which the International Union for Conservation of Nature (IUCN) Red List assessments have been carried out, 11 are currently classified as Threatened, and seven are listed as Critically Endangered (IUCN, 2019). Additionally, two recently revalidated African

species (*Crocodylus suchus* and *Mecistops leptorhynchus*) are awaiting formal conservation status assessment (Shirley et al., 2018; Isberg et al., 2019), but given their restricted ranges and increasing anthropogenic pressures they are likely to be classified as Critically Endangered (Shirley et al., 2009; Hekkala et al., 2011; Grigg and Kirshner, 2015; Shirley et al., 2018).

While the primary threat to the majority of crocodilian species is habitat loss (IUCN, 2019), many have also suffered from decades of unregulated hunting for skins and meat (Grigg and Kirshner, 2015). Conservation measures—including bans on hunting and harvesting of *A. mississippiensis* in southern USA and *C. porosus* in northern Australia implemented in the 1960s and 1970s—have allowed these populations to recover (Brandt, 1991; Elsey and Selman, 2010; Grigg and Kirshner, 2015). Rigorous monitoring of both species over several decades has provided the ecological data crucial for establishing successful ranching programs, and the economical benefits of sustainable use have ensured support for conservation of the species (Messel and Vorlicek, 1987; Brandt, 1991; Rice et al., 1999; Grigg and Kirshner, 2015). Many crocodilians can be dangerous to humans, with multiple fatal attacks occurring every year (CrocBite, 2019). Thus, human-wildlife conflict can pose a further challenge to conservation programmes, and communities living without wild predators for extended periods of time can be resistant to species reintroductions (Pooley et al., 2017). Monitoring crocodilians is therefore not only a tool for conservation management, but also for sustainable use and population control of dangerous animals (Bayliss, 1987).

However, while the biology, ecology and population dynamics of the economically valuable crocodilians, particularly in developed countries, have been relatively well-studied (Lang, 1976; Messel and Vorlicek, 1987; Webb et al., 1977; Taylor, 1979; Brandt, 1991; Read et al., 2007; Mazzotti et al., 2009), the species which are not considered commercially valuable have received less attention and support. Among the least-known taxa when it comes to basic ecology, are two genera inhabiting flooded forests and forested rivers: (i) from West and Central Africa, the African slender snouted crocodiles *Mecistops* with two species (*M. cataphractus* and *M. leptorhynchus*; Shirley et al., 2018); and (ii) the Southeast Asian genus *Tomistoma* comprising one species (the Sunda gharial, *T. schlegelii*; Bezuijen et al., 2014). In terms of conservation status, *M. cataphractus* is listed as Critically Endangered on the IUCN Red List of Threatened Species, while *T. schlegelii* is categorised as Vulnerable (IUCN, 2019).

The lack of information on these species poses a significant barrier for establishing biologically sound management programmes (Shirley, 2010a). Additionally, the information on population status of African dwarf crocodiles *Osteolaemus* spp., which are sympatric with *Mecistops* spp. and are currently classified as Vulnerable (Crocodile Specialist Group, 1996), has been largely gleaned from anecdotal reports (Eaton, 2010). As the animals are an important source of protein, particularly for the rural inhabitants in West and Central Africa, and feature prominently in bushmeat trade, surveys of their status and distribution across their range are considered as high priority according to the IUCN Crocodile Specialist Group Species Action Plan (Eaton, 2010).

Crocodilian monitoring projects to date have employed traditional visual survey methods, detecting animals using spotlights at night and through presence of animals, tracks, nests or faeces during the day (Bayliss, 1987; Simpson, 2006, also see Chapter 6.1). While successful when applied to some of the more conspicuous species, these methods are of less use when applied to animals that are wary and/or present in habitats with limited access. Previously hunted crocodiles are often difficult to detect; in such populations only young, naïve animals can be spotted using traditional spotlight survey methods, and due to high mortality rate (Hussain, 1999; Webb et al., 1983a; Somaweera et al., 2013) cannot provide reliable estimates of breeding population density (Grigg and Kirshner, 2015). Furthermore, dense vegetation can both limit observer access and conceal crocodilians (Ouboter, 1996a), thus differences in habitat and vegetation structure can introduce further bias to visual population assessment. Monitoring methods which employ the use of acoustic signals, through passive acoustic monitoring or acoustic lures, while not previously used on crocodilians, have been successful in monitoring shy, cryptic, nocturnal and forest-dwelling species, including marine mammals, bats, elephants, primates and birds (Blumstein et al., 2011; Browning et al., 2017; Wrege et al., 2017).

1.3 Rationale for the study

Crocodilians living in forests—where conspecifics may be less visible—likely rely on acoustic communication, particularly during mating and territory defence. However, in the three threatened genera which prefer forested habitats (*Mecistops*, *Osteolaemus* and *Tomistoma*) acoustic communication has not been studied beyond anecdotal reports of both *Mecistops* and *Osteolaemus* being somewhat vocal (Shirley, 2010a; Dinets, 2013b). In this thesis, I aimed to establish the adult vocal repertoires of the three genera, and test the use of acoustic-signal-based methods as alternatives to the standard spotlight survey monitoring techniques.

1.3.1 Thesis overview

- In Chapter 2, I introduce the two study sites in Africa (Gabon and Côte d'Ivoire), where data collection for Chapters 3, 5 and 6 took place. I also introduce the African crocodile species present at both sites, as well as the study species from Southeast Asia.

- In Chapter 3, I present the distribution and habitat preferences of the crocodiles present at the two African study sites. I demonstrate the habitat partitioning between the three sympatric species in Gabon and between the two species in Côte d'Ivoire, which can affect the species detection rates through different monitoring techniques.

- In Chapter 4, I compare adult African dwarf crocodiles (*Osteolaemus tetraspis*) vocalisations recorded in captivity with suspected *O. tetraspis* calls obtained through passive acoustic monitoring of wild forest elephants in Gabon, to determine if both belong to the same

species. I also identify and classify the acoustic repertoire of adult *O. tetraspis*, providing a baseline for the species acoustic identification.

- In Chapter 5, I describe and compare acoustic characteristics of West African slender-snouted crocodiles (*M. cataphractus*) produced by individuals of different body sizes. I examine the responses of smaller and larger *M. cataphractus* to distress call playback of conspecifics of different size classes, to determine which of the signals attract or repel other crocodiles.

- In Chapter 6, I test the use of two acoustic monitoring techniques—(i) passive acoustic monitoring; and (ii) playback surveys broadcasting *M. cataphractus* distress calls—to determine if either method improves *M. cataphractus* detection rates over the standard spotlight surveys.

- In Chapter 7, I present the first account of adult acoustic communication in a Southeast Asian forest-dwelling crocodilian, the Sunda gharial (*T. schlegelii*), which is produced during mating. I also provide the description of the courtship behaviour of this species.

- In Chapter 8, I summarise the implications of these results for biomonitoring and crocodile conservation, and then provide a perspective on the direction of further research.

CHAPTER 2

STUDY SITES AND STUDY SPECIES

The data presented in Chapters 3, 5 and 6 were collected during fieldwork in Central (Gabon) and West (Côte d'Ivoire) Africa between January and May 2018. In this chapter, I describe the two main field study sites in Africa, as well as all the study species featured in this thesis. The data presented in Chapters 4 and 7 were collected in captivity; details of these study sites are provided in the relevant chapters.

2.1 Study sites

2.1.1 Central Africa

Central Africa is home to the world's second largest contiguous rainforest, and 89% of the continent's tropical rainforest is located around the Congo basin (Mayaux et al., 2013). The Republic of Gabon is an important part of that block, with 80% of the country covered by tropical forest (Lee et al., 2006). Since 2002, 10.8% of Gabon's territory is protected through the formation of 13 national parks (Pauwels et al., 2006b) (Fig. 2.1). Further protected areas, including hunting reserves, faunal reserves, wildlife management areas and Ramsar Sites (Wetlands of International Importance) encompass additional 11.6% of the country (UNEP-WCMC and IUCN, 2018). The largest of these is the Gamba Complex, binding several earlier reserves in the industrial corridor between Loango and Moukalaba-Doudou national parks (Fig. 2.2) into an 11,320 km^2 protected area (Lee et al., 2006).

The variety of habitats found in the Gamba Complex—beaches and dunes at the coast, mangrove forests, scrubs, lowland and upland forests, rocky outcrops, secondary forests, savannah grasslands, papyrus and *Raphia* marshes, as well as freshwater and brackish wetlands and swamps—make this the most diverse protected area in Gabon (Lee et al., 2006). The dense forest

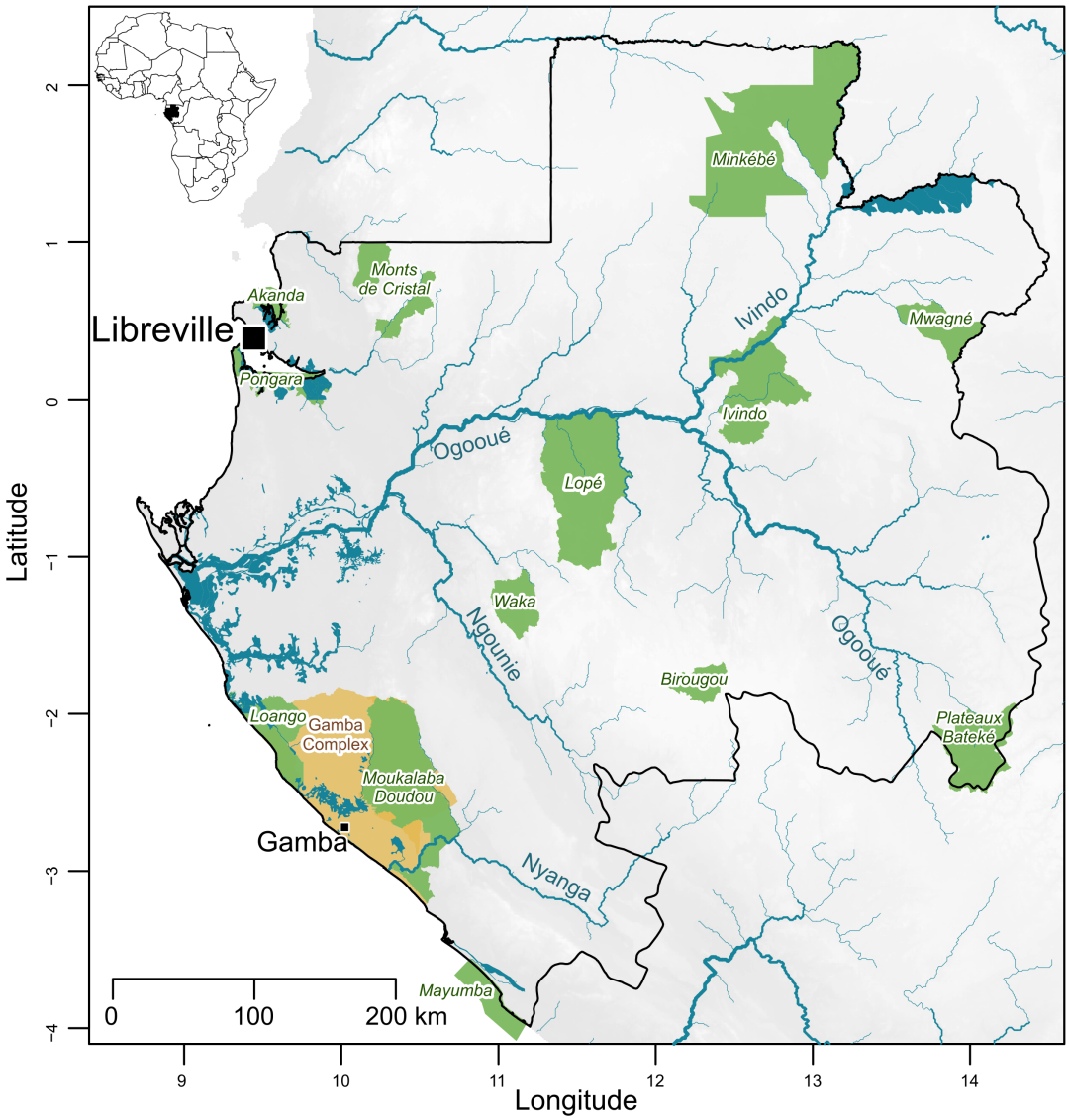

FIGURE 2.1. Locations of the 13 national parks established in Gabon (green) and the Gamba Complex of Protected Areas (orange) (data sources: Lehner et al., 2006; IUCN and UNEP-WCMC, 2018).

and mountainous regions of the Moukalaba-Doudou National Park at the eastern border of the Gamba Complex covers 4,500 km^2 and serves as an important refuge for western lowland gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes troglodytes*) (Lee et al., 2006). Loango National Park on the western border encompasses 1,550 km^2 of mosaic habitat and houses a range of megafauna, including forest elephants (*Loxodonta cyclotis*), gorillas, chimpanzees and hippopotamus (*Hippopotamus amphibious*) (Lee et al., 2006).

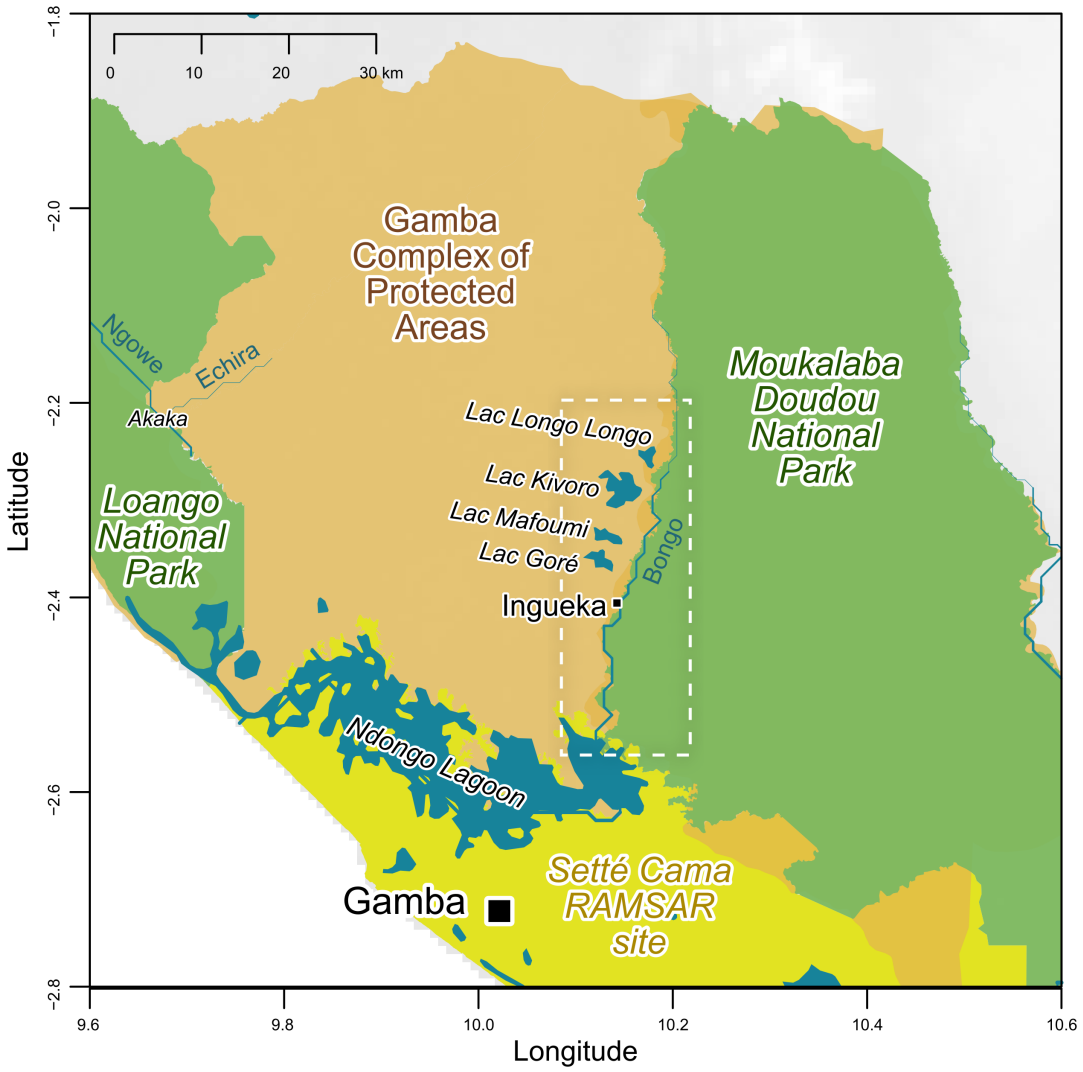

FIGURE 2.2. The Gamba Complex of Protected Areas, including Moukalaba-Doudou and Loango national parks and the Sette Cama Ramsar Site (data sources: Lehner et al., 2006; IUCN and UNEP-WCMC, 2018). White dashed line marks the study site in the Bongo river area.

The Gamba Complex has three main watersheds: the Nyanga River, the Ndongo Lagoon and the N'gové Lagoon, as well as many smaller rivers, streams, lakes and swamps forming a complex hydrological network (Lee et al., 2006). The river at the centre of my study site—Bongo

River, also known as Rembo Bongo—is the main tributary of the Ndongo Lagoon (Liwouwou et al., 2014). It flows for 200 km through the rainforest from Ingoumbi Mountains, and forms the western border of the Moukalaba-Doudou National Park (Fig. 2.2). Bongo River has several smaller tributaries and water bodies (Liwouwou et al., 2014), including four lakes which were part of my study site: Lac Longo Longo (−2.256172, 10.178823), Lac Kivoro (−2.288917, 10.155923), Lac Mafoumi (−2.341096, 10.143835) and Lac Goré (−2.375438, 10.136754), all surrounded by lowland forest (Fig. 2.2). The wetlands are inhabited by large aquatic vertebrates including hippopotamus, African manatee (*Trichechus senegalensis*) and three species of crocodilians: Nile crocodile (*Crocodylus niloticus*), Central African slender-snouted crocodile (*Mecistops leptorhynchus*) and dwarf crocodile (*Osteolaemus tetraspis*).

Human activity in the Gamba Complex has historically involved hunting, fishing, gathering, and agriculture practised by the settlers from the Congo (Lee et al., 2006). Fishing is practised in all the waterways, with several villages located around the lagoon and along Bongo River, using fishing as their main income. Since the discovery of oil fields in 1963, Gamba increased in size from a small fishing village to a town of around 8,000 inhabitants (Lee et al., 2006), mostly employed in roles supporting the activities of Shell Gabon until the company withdrew from the area in 2017. With the diminishing oil resources, the operations have been taken over by Assala Energy.

The dry season lasts from June to August, with a second, shorter dry season in January, though the precise patterns vary between the years (Lee et al., 2006), with the variation made more prominent by climate change. The average seasonal temperatures in the Gamba Complex are between 24–28°C, and annual rainfall measured in 1984–2002 ranged between 2,093–2,300 mm (Lee et al., 2006).

2.1.2 West Africa

The West African Forests are identified as one of the 25 biodiversity hotspots of the world (Myers et al., 2000). Taï National Park, located in the Southwest Côte d'Ivoire (Fig. 2.3), is one of the last large areas of primary forest in West Africa, covering around 3,500 km^2 (Waitkuwait, 1985). The Park has been listed as a World Heritage Site and is home to many large vertebrates, including chimpanzee (*Pan troglodytes verus*), pygmy hippopotamus (*Choeropsis liberiensis*), bush elephant (*Loxodonta africana*), and leopard (*Panthera pardus*) (Chatelain et al., 2001).

Taï National Park lies in the watershed between the Sassandra and Cavally rivers and contains their tributaries, which gather water from the Taï Forest (Waitkuwait, 1985). These include the Hana and Meno rivers, which flow into Cavally (Fig. 2.4). The water level in both Hana and Meno rivers varies seasonally, rising continuously during the rainy season, and remaining lower throughout the drier period. In the transition between dry and rainy season, their level may vary daily. The smaller tributaries such as Momo and Petit Hana, which flow into the Hana river, are dependent on local rainfall throughout the year (Waitkuwait, 1985). The river system is home

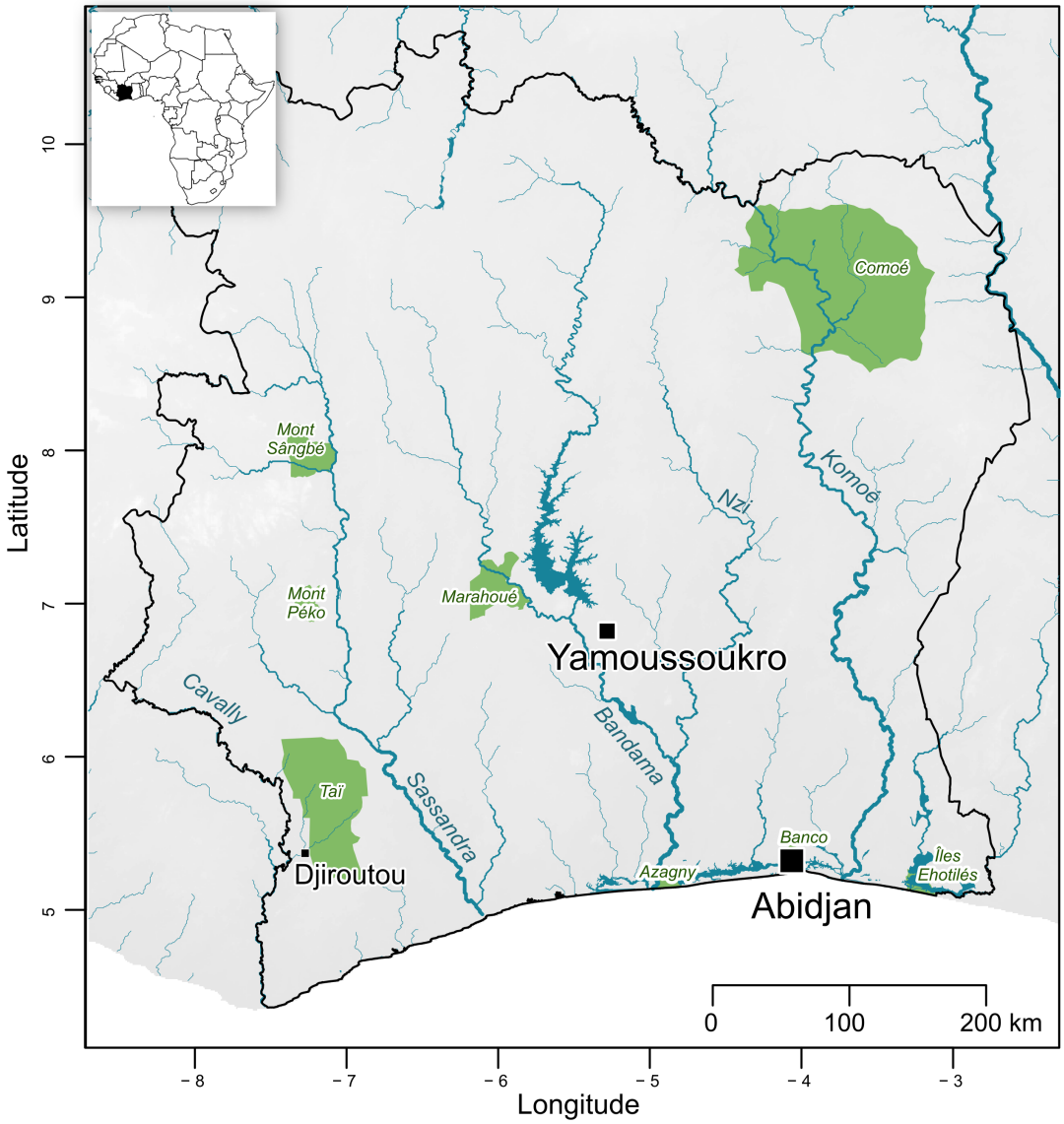

FIGURE 2.3. Locations of the national parks (green) in Côte d'Ivoire (data sources: Lehner et al., 2006; IUCN and UNEP-WCMC, 2018).

to two species of crocodiles: the West African slender-snouted crocodile *Mecistops cataphractus*, and the dwarf crocodile *Osteolaemus* aff. *tetraspis* (Chatelain et al., 2001).

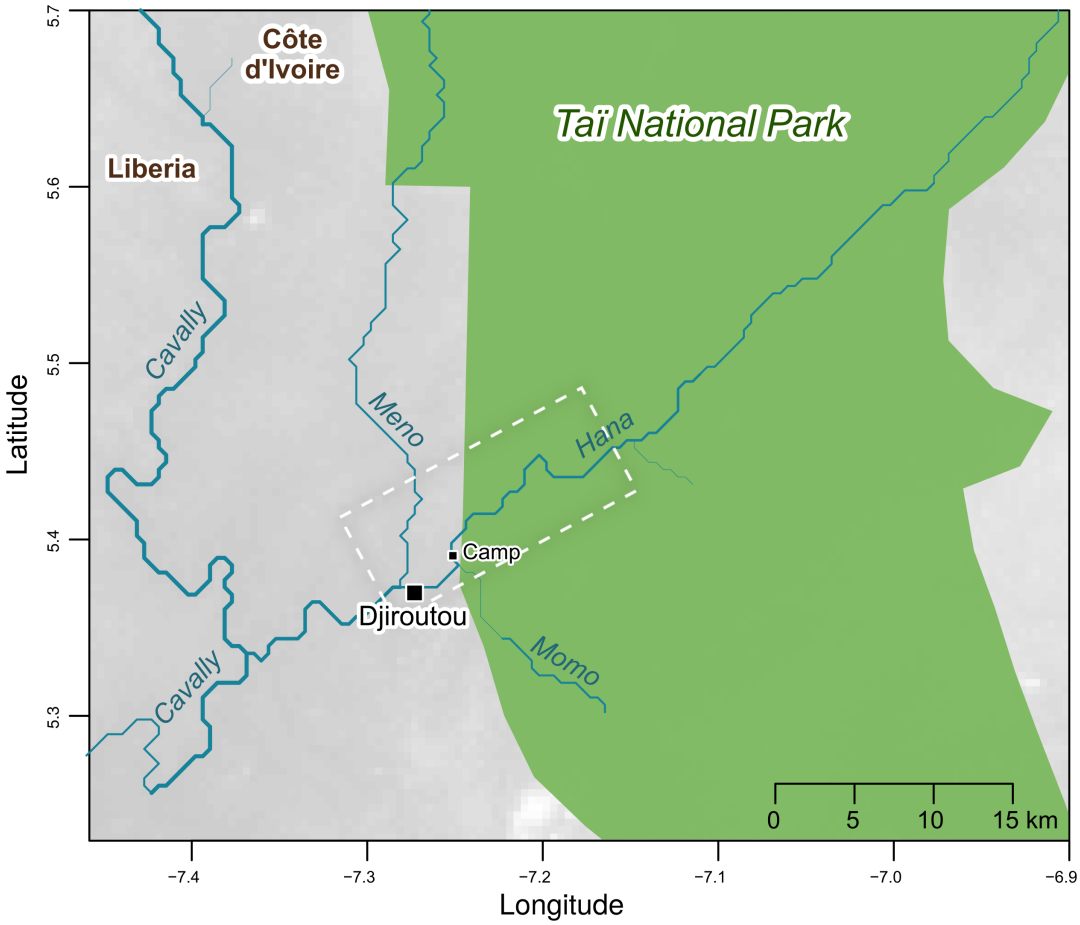

FIGURE 2.4. The river system in south-western Taï National Park near Djiroutou village (data sources: Lehner et al., 2006; IUCN and UNEP-WCMC, 2018). White dashed line marks the study site in the Hana and Meno river area. The location of the research camp (Ecotel Touraco) is marked as "Camp".

As the lead producer of the world cocoa crop, Côte d'Ivoire has undergone intense deforestation, with estimated degradation of at least 83% of the original forests, from 15 million ha in the early 1960s, to 2.5 million ha remaining in 1996 (Ruf et al., 2015; N'Gbala et al., 2017). West of Taï National Park, deforestation has progressed in stages, with the forest cover reduction from 89.6% in 1976 to 6.7% in 2003 (Chatelain et al., 2010). The areas immediately adjacent to the national park have been harvested for timber and are now used for cash crop cultivation, primarily cocoa (Chatelain et al., 2010). Apart from agriculture, fishing and hunting are sources of income for the local people (Kouassi et al., 2019), and pose threats to crocodile populations through prey depletion and accidental drowning in fishing nets and traps (Shirley et al., 2009). Although fishing inside or along the border of Taï National Park is prohibited, both illegal fishing and

poaching are still an issue, as bushmeat remains an important source of protein, particularly for poor families in the area (Kouassi et al., 2019). Illegal fishing nets, as well as evidence of poaching, can be found on occasion along the protected parts of the Hana River (Christine Kouman, pers. comm.), though the presence of researchers and tourists has reduced the poaching activities in the region (Campbell et al., 2011; N'Goran et al., 2012).

The dry season lasts from December to January, with a second, shorter drier period in July–August (Waitkuwait, 1985). The average temperature is between 24–27°C throughout the year, with the annual rainfall between 1,700–2,200 mm (Waitkuwait, 1985).

2.2 Study species

2.2.1 Slender-snouted crocodiles: *Mecistops* spp.

African slender-snouted crocodiles (genus *Mecistops*) are some of the rarest and least-studied crocodilians. The genus was assumed throughout the 20th century to comprise just a single species *Mecistops cataphractus* (Cuvier, 1824), inhabiting Western Africa across Upper Guinea through to the Congo Basin. Recent molecular and morphological studies, however, revealed that this name actually comprises two superficially similar species: the West African slender-snouted crocodile *Mecistops cataphractus* and the revalidated Central African slender-snouted crocodile *Mecistops leptorhynchus* (Bennett, 1835). These two species are biogeographically separated by the Cameroon Volcanic Line (Fig. 2.5; Shirley et al., 2014, 2018).

Mecistops cataphractus is found in the Upper Guinea region, its range extending through Côte d'Ivoire, The Gambia, Ghana, Liberia and Sierra Leone (Shirley, 2014; Shirley et al., 2018). In Côte d'Ivoire, populations of *M. cataphractus* can be found in and around Taï National Park (Fig. 2.6B; Waitkuwait, 1985), Azagny and Comoé national parks (Shirley et al., 2009), as well as many rivers throughout the country (Fig. 2.3; Shirley et al., 2018).

Mecistops leptorhynchus inhabits the Congolian bioregion, with a current confirmed range encompassing Central African Republic, Democratic Republic of Congo, Gabon, and Republic of Congo (Shirley et al., 2018). The largest number of confirmed reports are from Gabon, where *M. leptorhynchus* is found in the Oogué River, its delta tributaries, the Nyanga River, and the coastal lagoons and river systems south of the Oogué River delta (Shirley et al., 2018). The species can be found in Ivindo, Loango and Moukalaba-Doudou National Parks (Fig. 2.6A; Pauwels, 2006), including Lac Kivoro (Fig. 2.2; Pauwels et al., 2006b).

While several morphological features can be used to distinguish *M. cataphractus* from *M. leptorhynchus* (Shirley et al., 2018), the general morphology, body size and shape are similar for both species. The body of *Mecistops* is medium-sized, reaching 3–3.5 m (Shirley, 2010a), although individuals over 4 m long have been reported in the past (Trutnau and Sommerlad, 2006). The animals have a long narrow snout, and feed primarily on fish (Pauwels, 2007), but as with many crocodilians, they can take a variety of other prey items including medium-sized mammals

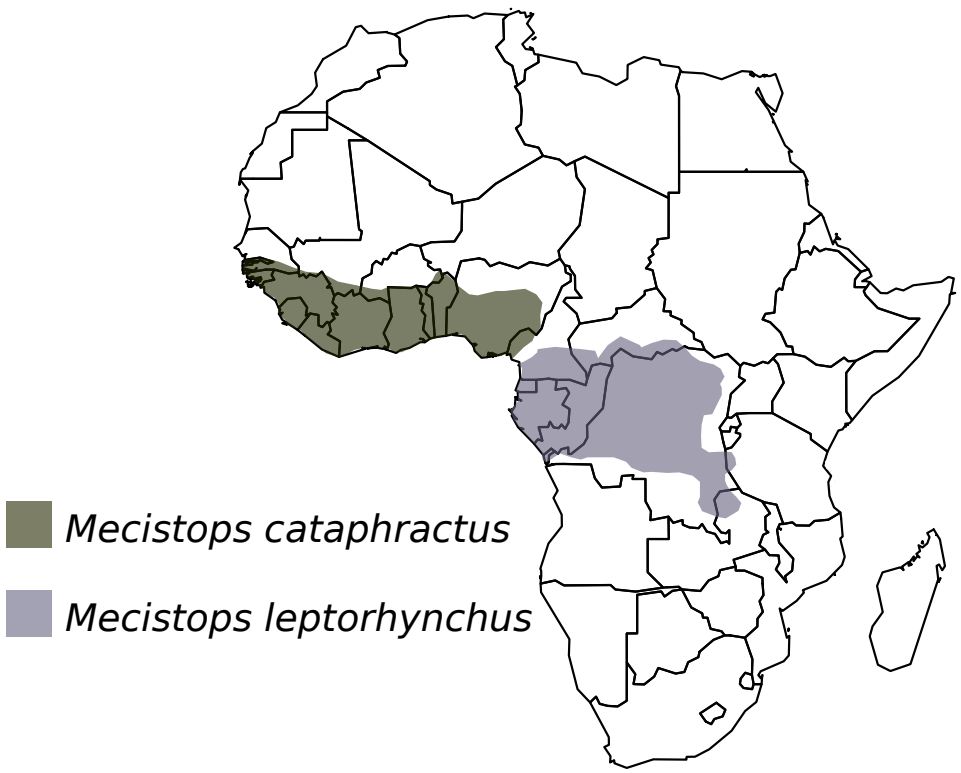

FIGURE 2.5. Distribution of the two African slender-snouted crocodile species (genus *Mecistops*). Redrawn from Shirley et al. (2015).

(Trutnau and Sommerlad, 2006; Shirley et al., 2018). Relatively little is known about *Mecistops* ecology in the wild. The animals prefer forested rivers and water bodies such as lagoons and lakes (Shirley, 2010a), but can also be found in more open river habitats with gallery forest (Shirley et al., 2009). Breeding begins with the onset of the rainy season (Waitkuwait, 1985). Females build mound nests on river shores and lay around 16 eggs (Shirley, 2010a), assist the young during hatching (Trutnau and Sommerlad, 2006), and may attend to the young for up to several months afterwards (Shirley et al., 2018). Anecdotal reports suggest that *Mecistops* are also very vocal species, particularly at the start and during the breeding season, but their communication and behavioural ecology have not been studied before (Shirley, 2010a; Shirley et al., 2018).

Although separate conservation assessments for *M. leptorhynchus* and *M. cataphractus* are yet to be published, both species assessed together as *Mecistops cataphractus* are listed as Critically Endangered on the IUCN Red List of Threatened Species (Shirley, 2014). The numbers of *M. leptorhynchus* in Central Africa are declining throughout the species range, with the exception of remote wetlands in Gabon that are suspected to harbour 70% of the species' remaining population (Shirley et al., 2018). The main threats to remaining *M. leptorhynchus* are subsistence fisheries, leading to reduced prey base and incidental drowning in fishing nets, as well as habitat modification for agricultural development (Shirley et al., 2018). In West Africa, *M.*

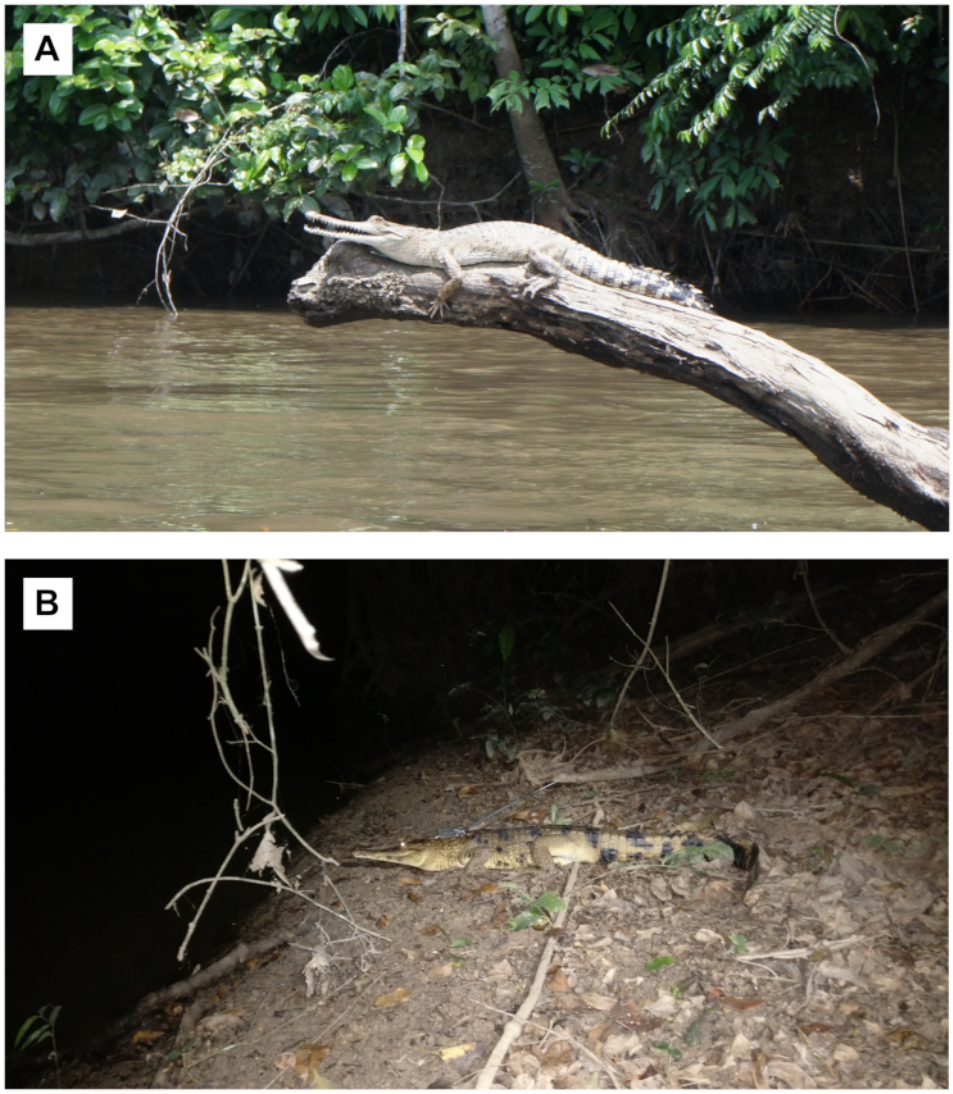

FIGURE 2.6. Photographs of wild slender-snouted crocodiles (*Mecistops* spp.) in Central and West Africa. Wild *M. leptorhynchus* basking on a log on the Bongo River, Gabon (A); wild *M. cataphractus* on the shore of Hana River in Taï National Park, Côte d'Ivoire (B).

cataphractus have declined due to habitat destruction and hunting, with remaining fragmented populations threatened with further habitat loss and small population effects (Shirley et al., 2018).

2.2.2 African dwarf crocodiles: *Osteolaemus* spp.

The African dwarf crocodiles (*Osteolaemus* spp.) are the smallest of the African crocodilians, reaching a maximum size of 1.8 m (Waitkuwait, 1989). The genus *Osteolaemus* comprises at least three species inhabiting swamps and flooded forests of Central and West Africa (Eaton et al., 2009): *O. osborni* in the Congo River basin, *O. tetraspis* in Oogué River basin, and *O.* aff. *tetraspis* in West Africa (Fig. 2.7).

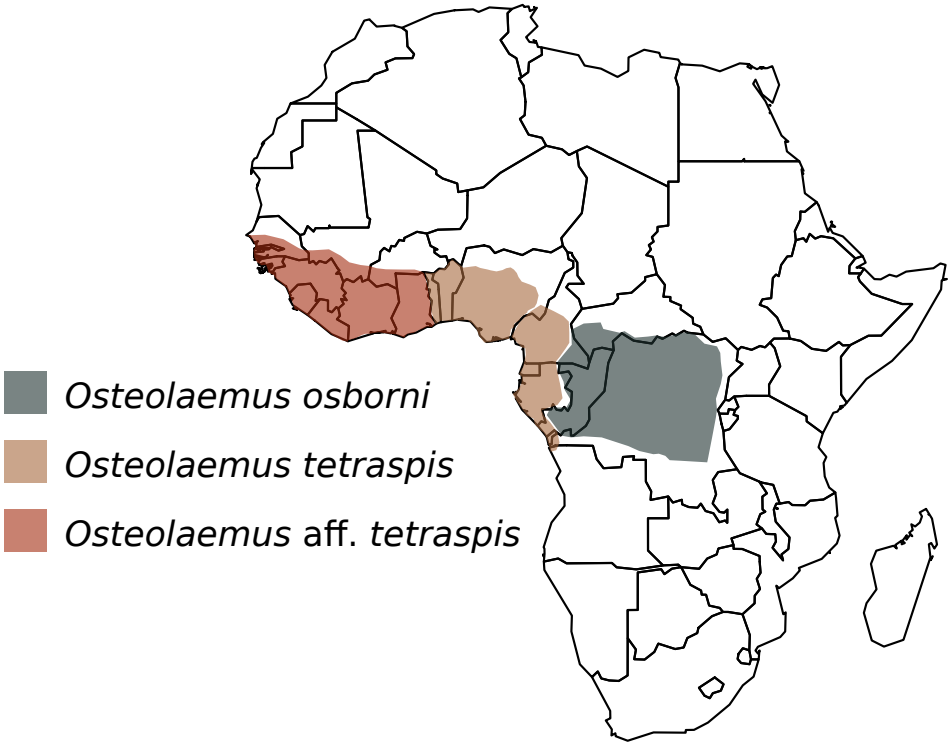

FIGURE 2.7. Distribution of the African dwarf crocodile species (genus *Osteolaemus*). Redrawn from Shirley et al. (2015).

In Gabon, *O. tetraspis* can be found in Akanda, Ivindo, Loango, Lopé, Minkébé, Pongera and Moukalaba-Doudou national parks (Fig. 2.8A; Pauwels, 2006; Shirley and Austin, 2017). Studies in Côte d'Ivoire recorded low density of *O.* aff. *tetraspis* but anecdotal reports indicate it is abundant throughout the country (Shirley et al., 2009), including a population in Taï National Park (Fig. 2.8B).

Only general information on *Osteolaemus* ecology is available, as none of the species have been sufficiently studied (Eaton, 2010). Dwarf crocodiles prefer dense swamps, flooded forests

and small streams under closed-canopy rainforest (Waitkuwait, 1989; Eaton, 2010). They are considered to be one of the more terrestrial crocodilians (Eaton, 2010; Shirley and Austin, 2017). *Osteolaemus tetraspis* are nocturnal (Eaton, 2010) and are generalist predators, feeding primarily on invertebrates and smaller vertebrates (Luiselli et al., 1999; Pauwels et al., 2007; Eaton, 2010). A recently discovered *O. tetraspis* population living exclusively in a cave system in Gabon has also adapted their diet to rely on bats and crickets (Shirley et al., 2016).

Very little is known about the behaviour and courtship in wild *O. tetraspis*. The breeding season overlaps with that of *Mecistops*, starting with the beginning of the rainy season (Waitkuwait, 1989; Kofron and Steiner, 1994). Females build mound nests on the forest floor and lay 10–14 eggs (Eaton, 2010).

The African dwarf crocodile (listed as *O. tetraspis*) is classed as Vulnerable on the IUCN Red List of Threatened Species, though their status, as well as taxonomy, need updating (Crocodile Specialist Group, 1996; Smolensky, 2015). The main threats include habitat loss, climate change, pollution, deforestation, as well as the bushmeat trade (Crocodile Specialist Group, 1996; Eaton, 2010). Dwarf crocodiles are common on the bushmeat market, and are a preferred game species for hunters as they can be easily transported alive to keep the meat fresh (Eaton, 2010).

2.2.3 Nile crocodile: *Crocodylus niloticus*

Nile crocodiles (*Crocodylus niloticus*) are the largest crocodilians in Africa, reaching up to 6 m in length (Trutnau and Sommerlad, 2006). They are found in a variety of habitats, ranging from lakes, rivers and swamps, to brackish wetlands and lagoons (Fergusson, 2010; Isberg et al., 2019). As generalist predators, they exhibit ontogenetic shift in prey, with hatchling and juveniles consuming mainly invertebrates, small fish and amphibians, while larger animals and adults feed on a variety of larger vertebrate prey, including humans (Wallace and Leslie, 2008; Pooley, 2016).

The Nile crocodile is the most broadly distributed crocodilian species on the continent, its range encompassing eastern and southern Africa, as well as the Atlantic coast from Gabon to Namibia (Fig. 2.9, 2.10; Shirley et al., 2015; Isberg et al., 2019). In Gabon the species is found only in the coastal regions of the Loango and Moukalaba-Doudou national parks, as well as the Gamba Complex (Pauwels, 2006). Nile crocodiles are not found in Côte d'Ivoire, where they are replaced by the West African crocodile, *Crocodylus suchus* (Hekkala et al., 2011).

Breeding occurs during the dry season (Kofron, 1991). The females dig holes in sandy banks, where they lay 35–50 eggs (Fergusson, 2010). They guard the nests and assist in hatching, protecting the young during the first weeks of their life (Fergusson, 2010; Chabert et al., 2015).

Nile crocodiles are listed as Least Concern on the IUCN Red List of Threatened Species, owing to their widespread range, despite some localised population declines (Isberg et al., 2019). Similarly to other crocodilians, *C. niloticus* face the threats of habitat loss, pollution, climate change, hunting for skins, but also the consequences of human-crocodile conflict (HCC) when

FIGURE 2.8. Wild *Osteolaemus tetraspis* (marked with the yellow arrow) entering the Bongo River, Gabon (A). Wild *O.* aff. *tetraspis* on the shore of Hana River in Taï National Park, Côte d'Ivoire (B).

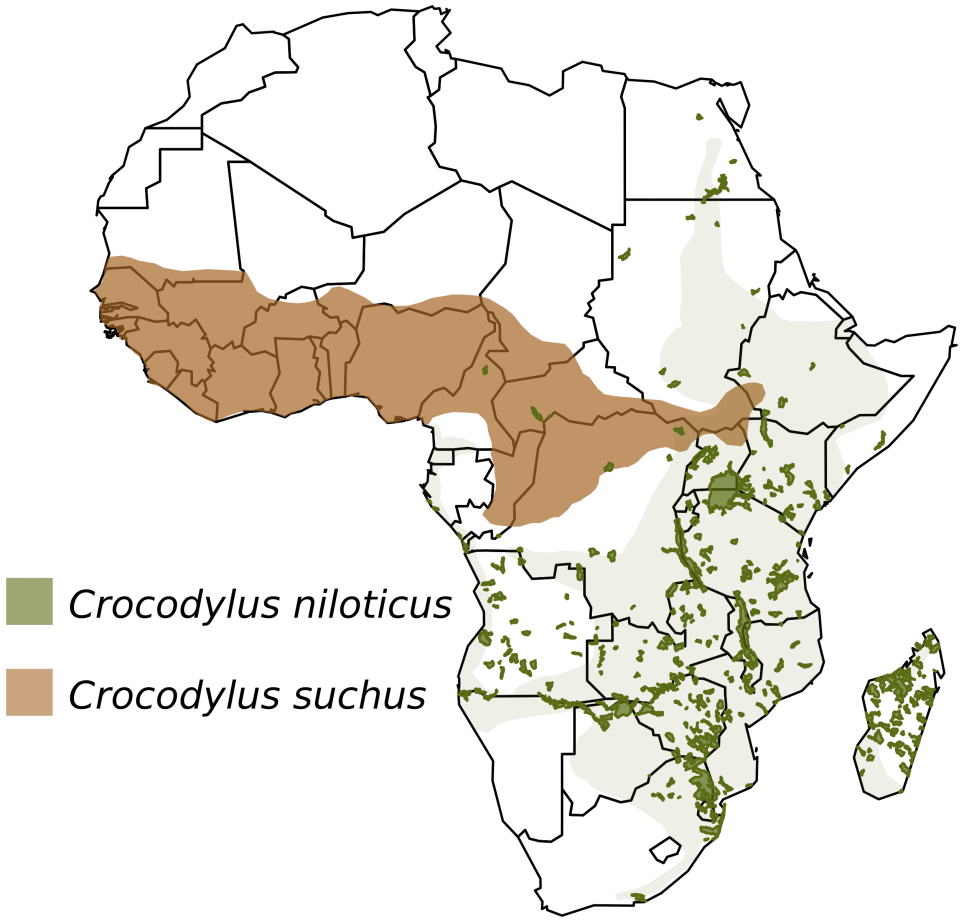

FIGURE 2.9. Distribution of the Nile crocodile *Crocodylus niloticus* (light green) and the West African crocodile *Crocodylus suchus* (orange), redrawn from Shirley et al. (2015). Updated, confirmed range locations of *C. niloticus* are marked in dark green. Source: Isberg et al. (2019).

people are at risk of predation (Pooley, 2016). The density of crocodiles is reported to be negatively correlated with human density, and populations have declined outside of the major protected areas (Fergusson, 2010).

2.2.4 Sunda gharial: *Tomistoma schlegelii*

Sunda gharials (*Tomistoma schlegelii*) are considered to be one of the rarest and least-studied crocodilian species. They are also among the largest, with adults reaching up to 5 m in body length (Trutnau and Sommerlad, 2006). They prefer peat swamp forests and freshwater wetlands (Bezuijen et al., 2001; Stuebing et al., 2006; Staniewicz et al., 2018) and are found in Malaysia (Peninsular Malaysia and Sarawak), Indonesia (Kalimantan, Sumatra and West Java) and Brunei (Fig. 2.11, 2.12; Stuebing et al., 2006; Bezuijen et al., 2014).

Little is known about the ecology and behaviour of *T. schlegelii* in the wild. Due to their long,

FIGURE 2.10. A wild *Crocodylus niloticus* in Kruger National Park, South Africa.

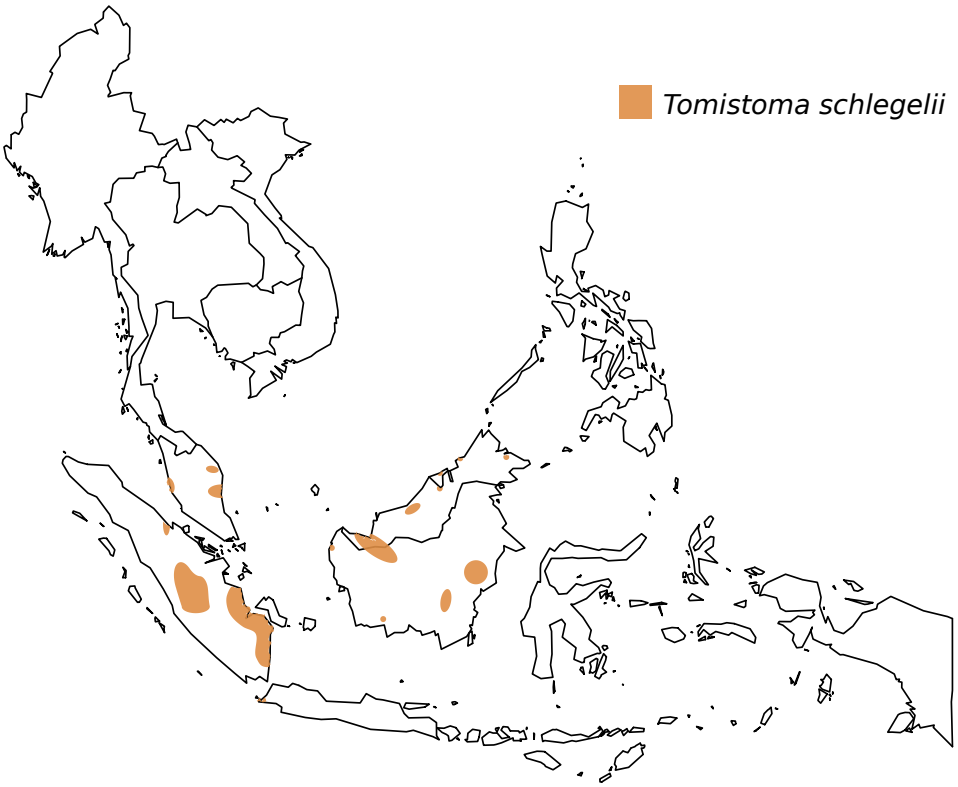

FIGURE 2.11. Distribution of the Sunda gharial *Tomistoma schlegelii* in Southeast Asia. Source: Bezuijen et al. (2014).

narrow snout, they have initially been thought to feed primarily on fish (Neill, 1971). However, limited reports (Galdikas, 1985; Bezuijen et al., 1997; Staniewicz et al., 2018) suggest that wild *T. schlegelii* can take a variety of prey, including primates, and the crocodile body size and prey availability may be the main limiting factor in prey choice (Staniewicz et al., 2018).

Information on breeding behaviour has largely been gleaned from incidental nest encounters in the wild and from observations of captive animals. Females build mound nests on land, usually at the base or near a tree, at the start of the dry season (Bezuijen et al., 1997; Ross et al., 1998; Staniewicz et al., 2018). The clutch size varies between 16–60 eggs (Bezuijen et al., 1997; Trutnau and Sommerlad, 2006) and the eggs are very large compared to other crocodilians, reaching 10 cm in length and 7.5 cm in width (Trutnau and Sommerlad, 2006). During incubation, which lasts 72–90 days (Trutnau and Sommerlad, 2006), the female may attend the nest and defend it from intruders (Rob Stuebing, pers. comm.), but there is no information on parental care during or after hatching.

There are currently no global estimates for the numbers of *T. schlegelii* left in the wild, and the species is classified as Vulnerable on the IUCN Red List (Bezuijen et al., 2014). Habitat loss resulting from swamp drainage, conversion to agricultural land, illegal logging and forest fires are the main threats to the species' survival (Bezuijen et al., 2014).

FIGURE 2.12. A captive *Tomistoma schlegelii* at Jong's Crocodile Farm, Malaysia.

CHAPTER 3

COMPARING THE HABITAT PREFERENCES OF SYMPATRIC CROCODILIANS IN MOUKALABA-DOUDOU NATIONAL PARK (GABON) AND TAÏ NATIONAL PARK (CÔTE D'IVOIRE)

Abstract

To avoid competition for resources, sympatric species separate into different niches and habitat partitioning is common in crocodilians with overlapping distribution ranges. African slender-snouted crocodiles *Mecistops* spp. are sympatric with dwarf crocodiles *Osteolaemus* spp., and in some parts of their range also with *Crocodylus* spp. I surveyed three aquatic habitat types (lagoon, lakes and river) in the protected area of the Bongo River region in Gabon, and the river within and outside of Taï National Park in Côte d'Ivoire, in order to determine the crocodile species distributions, and identify the features in the available habitat that are selected by each species. *Mecistops* spp. were the most frequently encountered crocodilians in all habitats surveyed, comprising 83% (n = 290) of all sightings identified to species in Gabon and 96% (n = 125) in Côte d'Ivoire. In both countries they preferred areas with greater vegetation cover, and were predominantly found in the shallow water near forested banks. Habitat partitioning between the sympatric crocodilians was observed in both countries. In Gabon, where *C. niloticus* was present, 92% (n = 33) of its sightings were in the lagoon, with *C. niloticus* preferring areas near grassland and papyrus, flatter banks and greater vegetation cover. *Osteolaemus tetraspis* (Gabon) and *O.* aff. *tetraspis* (Côte d'Ivoire) were rarely encountered (*O. tetraspis* n = 23; *O.* aff. *tetraspis* n = 5), and were primarily found on the shore, in the forest with dense vegetation cover. These results are consistent with the species preferences reported from other areas, and suggest low overlap in habitat use between *Mecistops* and *Osteolaemus* spp. in both study sites. As the terrestrial and aquatic habitats preferred by the two genera require different survey techniques, monitoring methods targetting population density of one of them might not give accurate information on the other.

3.1 Introduction

Crocodilians are found in diverse aquatic habitats, including lakes, rivers, canals, lagoons, streams, marshes and wetlands across the tropical and subtropical regions. Throughout these areas, most of the 28 currently recognised species overlap with one or more other crocodilian (Grigg and Kirshner, 2015; Shirley et al., 2018), forming at least 34 sympatric pairs (Ouboter, 1996b; Shirley and Austin, 2017; Staniewicz et al., 2018).

In order to avoid competition, sympatric species separate into different resource niches (Pianka, 1994). Crocodilians with overlapping range distributions often have dramatically different snout shapes and morphology, ranging from long and narrow (longirostrine) to relatively short and broad (brevirostrine), which, often combined with different adult body size, allows them to specialise on different types of prey (Busbey, 1995; Pearcy, 2011). For example, the piscivorous, narrow-snouted *Gavialis gangeticus* is sympatric with the much more generalist and broad-snouted *Crocodylus palustris* (Rao and Choudhury, 1992), while the longirostrine *Crocodylus johnstoni* overlaps in range with the larger, brevirostrine *Crocodylus porosus* (Webb et al., 1983b). Despite the geographic overlap, competition between the sympatric crocodilians can be limited not only due to differences in diet, but also in preferred habitat (Magnusson et al., 1987; Staniewicz et al., 2018), nesting sites (Choudhary et al., 2018), breeding season (Webb et al., 1983a) or other life history traits, resulting in many of the sympatric crocodilians not being syntopic (Ouboter, 1996b; Grigg and Kirshner, 2015). However, even with the apparent niche partitioning, competition with the overlapping species may still exist and have a negative effect. For example, in areas with high caiman density and high productivity, *Melanosuchus niger* grow slower than the sympatric *Caiman crocodilus* in comparison to areas with lower crocodilian density (Da Silveira et al., 2013). Moreover, direct predation can also affect the overlapping species, and for example, in areas where they are sympatric, larger more aggressive *C. porosus* can kill *C. johnstoni* (Somaweera et al., 2013). Interactions between sympatric crocodilians can thus affect the populations of each species, but the extent of these effects is often not known (Somaweera et al., 2019).

In recent years, the taxonomy of African crocodilians has undergone significant changes. Historically, crocodilians in Africa were thought to belong to three species: the Nile crocodile *Crocodylus niloticus*, slender-snouted crocodile *Mecistops cataphractus* and dwarf crocodile *Osteolaemus tetraspis*, all overlapping in some parts of their geographical ranges (Waitkuwait, 1989; Trutnau and Sommerlad, 2006). Recent molecular studies have identified multiple allopatric "cryptic" species. The range of Nile crocodiles *C. niloticus* spans across East and Southern Africa, as well as the coastline of Angola and Gabon, while the *Crocodylus* sp. in West and Central Africa is the recently resurrected West African crocodile *C. suchus* (Fig. 2.9; Hekkala et al., 2011). West African slender-snouted crocodiles *M. cataphractus* are found in the Upper Guinea region (Fig. 2.5; Shirley et al., 2018), and are sympatric with *C. suchus* and the West African dwarf crocodile *Osteolaemus* aff. *tetraspis*, which is currently awaiting formal description (Fig. 2.7;

Eaton et al., 2009; Smolensky et al., 2015). The Central African slender-snouted crocodiles (*M. leptorhynchus*) occur in Central Africa (Fig. 2.5; Shirley et al., 2018), and are sympatric with the two dwarf crocodile species: *Osteolaemus osborni* in the Congo basin and the nominal African dwarf crocodile *O. tetraspis* in Oogué basin (Fig. 2.7), as well as with *C. niloticus* along the coast of Gabon and *C. suchus* in Central Africa (Fig. 2.9; Eaton et al., 2009; Smolensky et al., 2015).

The three genera, while sympatric, differ greatly in body size, snout morphology and ecology. *Crocodylus niloticus* can reach up to 6 m in length (Trutnau and Sommerlad, 2006) and are among the largest predators on the continent. Together with *Osteolaemus* spp., they are brevirostrine, but the latter are much smaller in size, with adults reaching up to 1.8 m (Waitkuwait, 1989). The longirostrine *Mecistops* are medium-sized crocodiles, growing up to 3–3.5 m long (Shirley, 2010a). While *Mecistops* overlap with *Osteolaemus* across their entire distribution range, Waitkuwait (1989) suggested niche partitioning between these sympatric crocodilians, including both the Upper Guinea species and the Congo basin species group. *Mecistops* spp. have been reported to prefer more continuous aquatic habitat and are found in forest-fringed rivers and lakes, and although they can be encountered in the same area, *Osteolaemus* spp. are thought to be more terrestrial, primarily inhabiting more isolated streams and swamps in the forest interior (Waitkuwait, 1989; Eaton, 2010; Shirley et al., 2018).

Despite a recent increase in publications (Pauwels, 2007; Eaton et al., 2009; Smolensky, 2015; Shirley et al., 2016, 2018), the crocodiles in West and Central Africa, particularly both *Mecistops* spp., remain some of the least-studied crocodilians, with few published peer-review papers on the ecology and behaviour of the recently revalidated species (Shirley et al., 2018). Their relationship with the sympatric *Crocodylus* also remains unclear, and while Shirley et al. (2009) and Fergusson (2010) suggested competition and niche partitioning with *M. cataphractus* and *O.* aff. *tetraspis* as the reason behind the limited syntopy and low density of *C. suchus* in West Africa, there are no published studies examining the competition between *C. niloticus* and sympatric crocodilians.

Understanding species ecology, distribution and habitat preferences is vital for conservation management. In the case of sympatric species, particularly apex predators such as crocodilians, the interactions between the species can affect their ecology, and conservation efforts targeting one species can impact those that are sympatric (Webb et al., 1983b; Somaweera et al., 2019). *Mecistops cataphractus* is listed as Critically Endangered on the IUCN Red List of Threatened Species (Shirley, 2014), and although the recently revalidated *M. leptorhynchus* is yet to be formally assessed (Shirley et al., 2018), as a subset of the former *M. cataphractus* its status is likely to be the same. The dwarf crocodiles *Osteolaemus* spp., while in need of an assessment review and update, are currently listed as Vulnerable (Crocodile Specialist Group, 1996). Although *C. niloticus* is classified as Least Concern, the population in Gabon is small and depleted, estimated to consist of fewer than 500 individuals (Isberg et al., 2019).

In this chapter, I examine the habitat preferences of two sympatric crocodilian groups, one

with three species (*C. niloticus*, *M. leptorhynchus* and *O. tetraspis* in the Bongo River region of Gabon) and one with two species (*M. cataphractus* and *O.* aff. *tetraspis* in the south-western Taï National Park in Côte d'Ivoire), during the rainy season. I compare my results to preliminary surveys conducted in Taï National Park in 1986 (Waitkuwait, 1989) and in the Bongo River region in 2009–2010 (Shirley, 2010b), and determine the habitat parameters that can predict species distribution in the study areas, as well as the extent of habitat partitioning between the species. The resulting species encounter maps at the study sites provide a baseline for species distribution, and a tool needed to evaluate the effectiveness of acoustic monitoring as alternative survey method in areas where multiple crocodilian species coexist.

3.2 Methods

General information on the study sites and species are presented in Chapter 2.

The Central African study site was in the Bongo River region of the Gamba Complex, Gabon (−2.432000, 10.132291). It encompassed the 28.9 km^2 of the northern area of Ndongo Lagoon (67.1 km perimeter), the Bongo River (57.6 km) and four lakes west of Moukalaba-Doudou National Park: Longo Longo (1.7 km^2, 17.5 km perimeter), Kivoro (7.7 km^2, 42.1 km perimeter), Mafoumi (4.5 km^2, 18.8 km perimeter) and Goré (6.4 km^2, 33.4 km perimeter) (Fig. 2.2). The shores of the northern Ndongo Lagoon were composed of mixed habitats, including lowland forest, savannah grasslands, papyrus and Raffia palm (*Raphia* sp.) marshes. The river and lakes were primarily surrounded by the lowland forest, although Raffia palms grow along the first 6 km upriver from the mouth of the Bongo (Fig. 3.1). I collected data during the rainy season (23 January to 24 February 2018), which corresponded with the predicted breeding season of *M. leptorhynchus* and *O. tetraspis*.

In West Africa, the study site was located near the south-western edge of Taï National Park, Côte d'Ivoire (5.389406, −7.25214). It included the Hana River flowing through the forest interior of the National Park (9.4 km), the border of the Park separating the forest from the agricultural land (8.1 km), as well as the cocoa plantation area (5.7 km) and Djiroutou village (Fig. 2.4, 3.2). An additional 3.9 km of the Meno River, a tributary of Hana, which flows through agricultural land, was also surveyed. I collected data during the start of the rainy season (11 April to 12 May 2018), which corresponded with the predicted onset of the breeding season for *M. cataphractus* and *O.* aff. *tetraspis*.

3.2.1 Crocodile surveys

To identify the crocodiles in the Bongo River area (Gabon), I conducted repeated spotlight surveys on 12 nights from a motor boat, travelling 25.1 ± 10.5 km per night between 1900 and 0400 hours. I surveyed a total of 204 km in the three main habitat types: the Bongo River (37.8 km), the lakes (106.4 km) and the northern part of the Ndongo Lagoon (58.9 km).

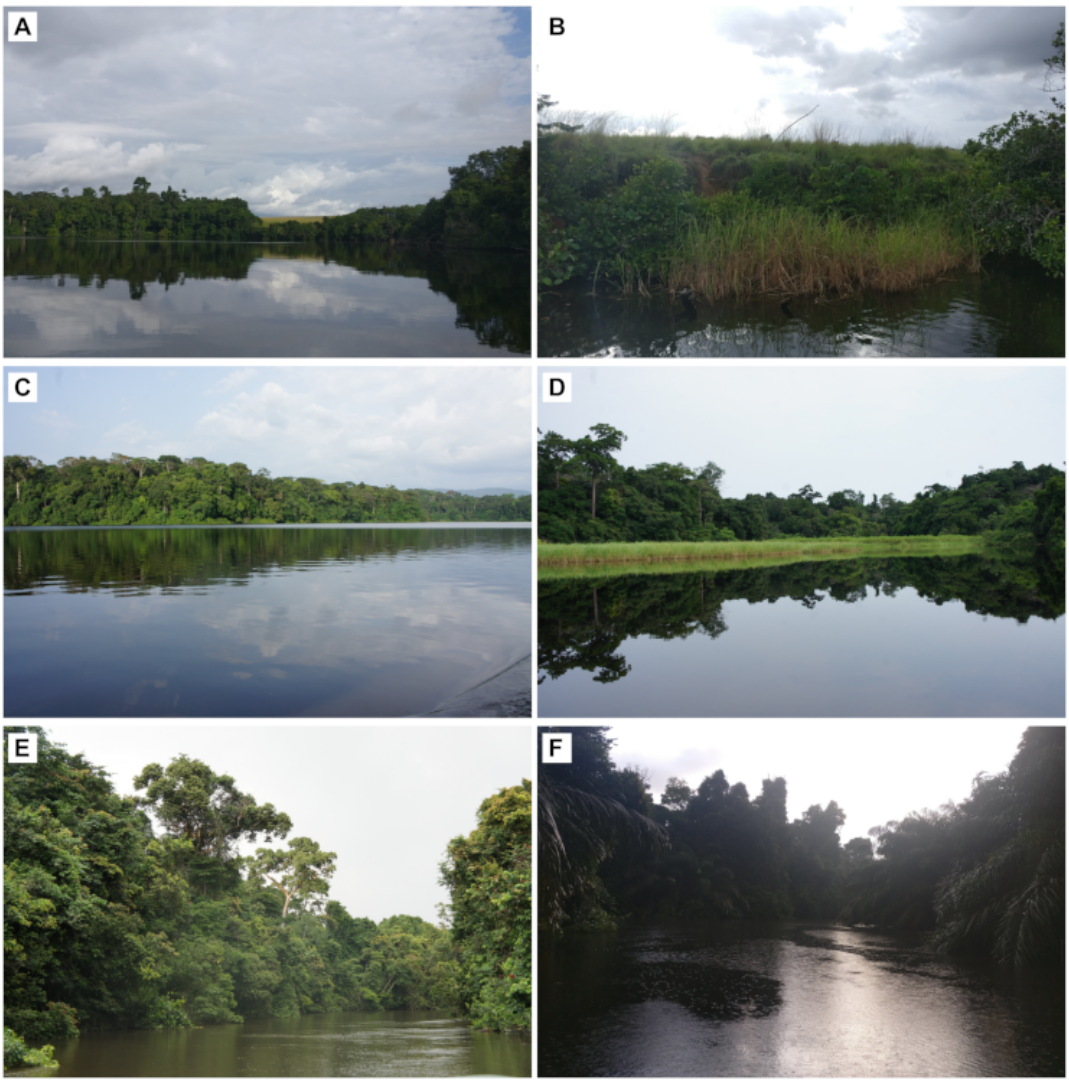

FIGURE 3.1. The three main habitat types in the Bongo River region (Gabon) with examples of some of the shore vegetation types: lagoon with forest shore and a fragment of grassland savannah visible behind it (A); grassland shore of the lagoon, with a visible crocodile path (B); forest along the shore of the lake (C); floating grass mat (left) and papyrus (right) at the shore of the lake (D); forest along the river (E); and Raffia palms palms along the river (F).

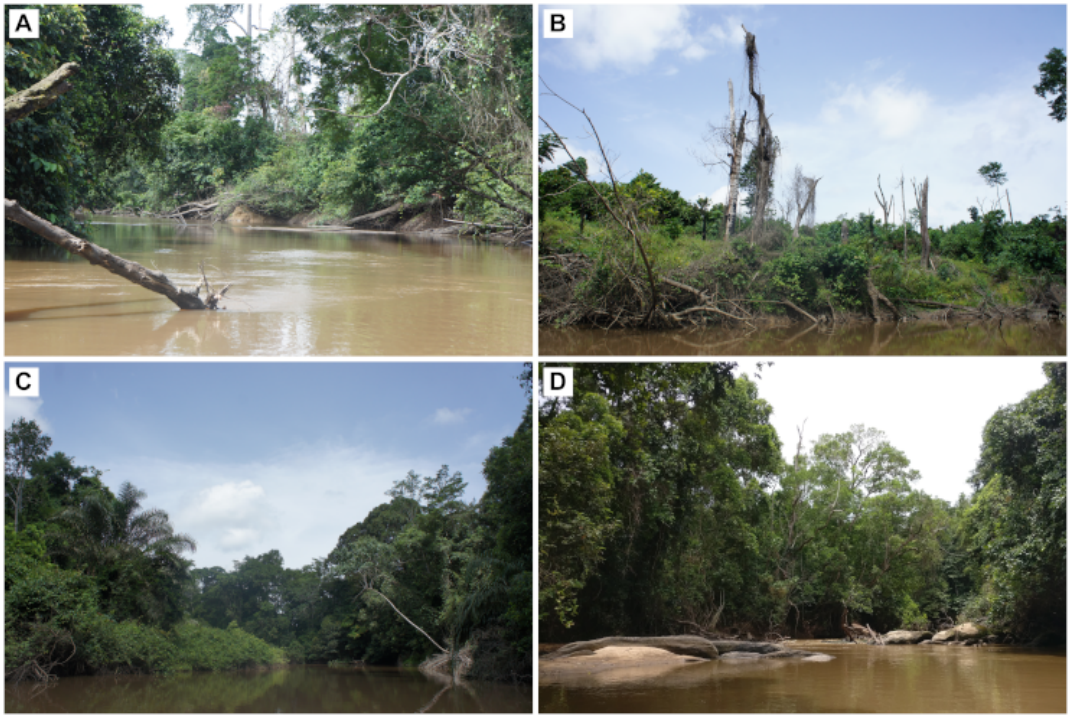

FIGURE 3.2. Hana River (Côte d'Ivoire) outside of the protected zone (A), with example of the forest shore converted to plantation area (B); along the border of Taï National Park (C) and in the interior of the park (D).

In Taï National Park (Côte d'Ivoire), I carried out 9 spotlight surveys from an inflatable boat with an outboard, travelling 14.1 ± 7.6 km per night between 1900 and 0500 hours and repeatedly surveying 27.1 km of the river habitat. To minimise the differences in crocodile detectability due to varying weather conditions and visibility, each site was surveyed twice on different nights in Gabon, and three times on different nights in Côte d'Ivoire.

Upon spotting a crocodile, I approached the animal and identified it to species or recorded it as "eyeshine only" (EO) if species identification was not possible. I logged the position of each crocodile with a Garmin GPSMAP 64s handheld GPS. I also estimated the animal's size to the nearest 10 cm and recorded the habitat parameters at each crocodile location (Table 3.1).

3.2.2 Habitat surveys

To identify the characteristics of available habitat in the Bongo River area, I conducted daytime habitat transects with the boat. Each transect was a 2 km section of the waterways that were surveyed for crocodiles at night, along the river (15.3 km total) and the shores of lakes (14.3 km total) and the lagoon (12.7 km total) (Fig. 3.3). I selected the transect sections in each main habitat at random, using portions of the GPS tracks displayed in Garmin Basecamp 4.6.01 software (Garmin, 2018). I recorded habitat parameters (Table 3.1) at 100 m interval points along

TABLE 3.1. Habitat characteristics measured at each point of a crocodile sighting and of the habitat survey transects. Shore habitat variable was classified in Gabon only, due to the larger study area containing a greater variety of aquatic and shore habitat types. Vegetation type was classified in Côte d'Ivoire only, as the study site was composed of only one type of aquatic habitat.

Variables	**Data type**	**Description and measurement details**
Main habitat type	Categorical	"Lagoon", "lake" or "river" in Gabon. "River" only in Côte d'Ivoire, but divided into "National Park interior", "Park border" and "plantation" zones.
Shore habitat	Categorical	In Gabon only. Identified the main type of the nearest shore vegetation: "forest", "grassland", "Raffia palm", and "papyrus".
Water level (m)	Continuous	In Gabon, I measured the depth of the water to the nearest 0.1 m using a weighted tape measure. In Côte d'Ivoire I used the Garmin Striker 4 Fishfinder to measure the water level to the nearest 0.1 m.
Vegetation cover (%)	Continuous	Approximate percentage of the 2 m radius area around the survey/crocodile location point covered by vegetation. Estimated by eye.
Vegetation type	Categorical	In Côte d'Ivoire only. Identified the type of nearest vegetation: "bamboo", "low-canopy tree/bush", "grass", "Raffia palm", "papyrus", "high-canopy tree".
Distance to vegetation (m)	Continuous	Distance to the nearest vegetation measured with the Shotsaver S400 laser rangefinder.
Distance to shore (m)	Continuous	Distance to the nearest shore measured with the Shotsaver S400 laser rangefinder. Measurements from land to the water shore were expressed as negative values.
Bank slope (degrees)	Continuous	Slope assessment, from flat (0) to steep (90), estimated by eye.

each transect ($n = 423$).

Where precise distance measurements at the transects point were not possible due to fast river flow or restricted access for the large survey boat, I measured the distance from the boat to the nearest vegetation (B_v) and to land (B_l), and measured the distance from the survey point to the nearest vegetation (P_v) on the Bing Satellite map projection using QGIS 3.8 software (QGIS Team Development, 2019). I then calculated the distance to land from the survey point (P_l) using: $P_l = B_l - (B_v - P_v)$. Where precise river water depth measurements were not possible due to deep and fast flowing water, I used the estimated average 4 m depth as the water level measurement for that point, obtained through measurements of river water depth at ten points with slow current.

In Taï National Park, I selected eleven 1 km long transect sections at random for each of the river sections, using portions of the GPS tracks displayed in Garmin Basecamp 4.6.01 software (Garmin, 2018). I recorded habitat parameters at 100 m intervals over 110 habitat points in total

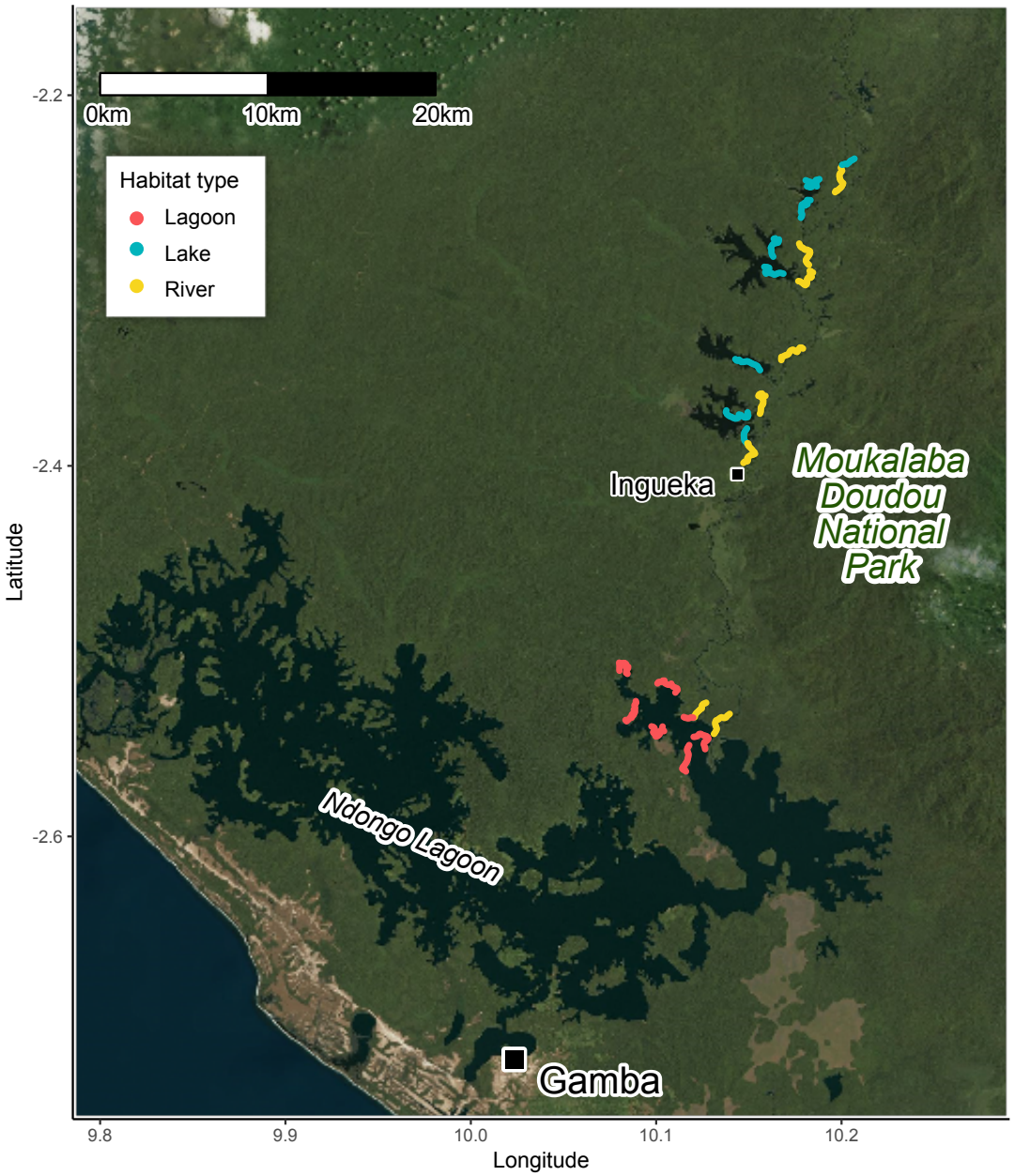

FIGURE 3.3. The 22 habitat transects conducted in the Bongo River region (Gabon) divided into the main habitat types: river (yellow), lake (blue) and lagoon (red). Base map: Bing Aerial.

on the Hana River inside the national park (4 km), along the border (3 km), and on the Hana and Meno rivers in the plantation area (4 km) (Fig. 3.4). The smaller boat and sonar allowed for precise habitat measurements at all points.

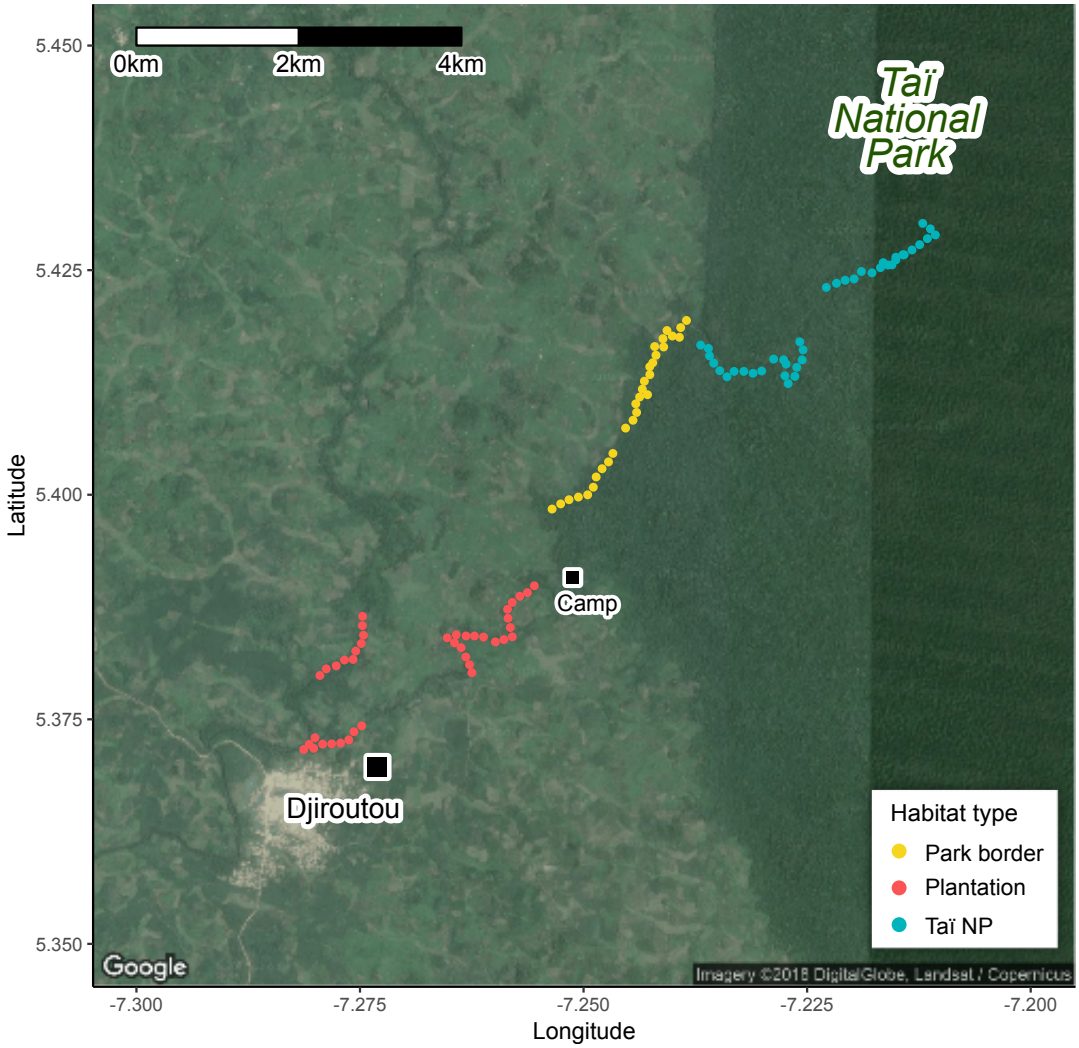

FIGURE 3.4. The 11 river habitat transects conducted in Taï National Park area (Côte d'Ivoire) divided into the plantation zone, national park border and national park interior. Base map: Google Satellite.

3.2.3 Statistical analysis

Only crocodiles confirmed to species were used in the analysis. The body size estimates of all encountered crocodiles were pooled into three categories: small (hatchlings/yearlings, < 60 cm total body length), medium (including juvenile/subadult *Crocodylus* and *Mecistops*, as well as adult *Osteolaemus*, 61–200 cm total body length), and large (> 200 cm total body length). Possible

repeated sightings of the same crocodiles on different nights were treated as independent habitat selection events in the analysis. All statistical analyses were carried out using R 3.6.0 statistical software (R Core Team, 2018).

3.2.3.1 Habitat selection analysis of Gabon data

I used a chi-square test to compare the distribution of species between the lagoon, lakes and river. In order to compare the numbers of encounters with crocodiles of different sizes between the three habitat types, I performed chi-square tests of each of the three size classes.

Due to the large survey area and differences in habitat composition between the lagoon, lakes and river, I analysed the habitat feature preferences for each of the three habitat types separately. To determine which of the continuous and categorical variables influence habitat selection in the sympatric crocodiles, I used a multinomial logistic regression (*multinom* function in NNET package) (Venables and Ripley, 2002) with the habitat survey values set as baseline for comparison to those of each of the species found in the area. Using the stepwise model selection (*stepAIC* function in MASS package) (Venables and Ripley, 2002), I chose the model with the lowest Akaike information criterion (AIC) as best.

To determine differences in habitat preferences between the species within each habitat type, I used Kruskal-Wallis tests to compare each of the continuous habitat features. As the lagoon had a diverse shore habitat, I used the chi-square test to compare shore habitat preferences between the three species present there.

3.2.3.2 Habitat selection analysis of Côte d'Ivoire data

To compare the numbers of encounters with *M. cataphractus* of different sizes between the National Park interior, its border and the agricultural area, I performed chi-square tests of each of the three size classes.

I used Kruskal-Wallis tests to compare the continuous habitat features at habitat transect points between the three river sections and a chi-square test to compare the types of the nearest vegetation to the survey points. While the plantation section of the river had significantly more bushes/low canopy trees and Raffia palms as the nearest vegetation type to the survey point than the Taï National Park border and interior, other habitat variables did not differ significantly between the three river sections (see Appendix A, Table A.1). As the river presented 27.1 km of continuous habitat for the crocodiles, whom were free to move between the protected and unprotected sections, the entire river habitat was used in the subsequent habitat selection analysis. In order to determine which of the continuous and categorical variables influence river habitat selection in the sympatric crocodiles, I used a multinomial logistic regression as with the Gabon analysis, and with the habitat survey values set as baseline for comparison to those of each of the species found in the Hana and Meno rivers. Again I chose the model with the lowest AIC as best.

To determine differences in habitat preferences between the two species, I used Mann-Whitney tests to compare each of the continuous habitat features. To determine differences in habitat preferences between *M. cataphractus* found at different river section, I used Kruskal-Wallis tests to compare the continuous habitat features, and chi-square test to compare the types of the nearest vegetation present.

3.3 Results

3.3.1 Bongo River region, Gabon

3.3.1.1 Species and size distribution of crocodiles

All three species of crocodiles found in Gabon were present in the Bongo River area (Fig. 3.5). In total, 349 sightings (36 *C. niloticus*, 290 *M. leptorhynchus* and 23 *O. tetraspis*) were confirmed during the study period. The species distribution differed significantly between the three main habitat types (the lagoon, lakes and river: $\chi^2 = 34.629$, df = 4, $P < 0.001$). *Mecistops leptorhynchus* was the most abundant species in all three habitats, while *C. niloticus* was found primarily in the lagoon (91.7% of the sightings) and not encountered in the lakes (Table 3.2).

TABLE 3.2. Numbers of crocodile sightings confirmed to species in the northern Ndongo Lagoon, the lakes and the Bongo River habitats (Gabon). Percentages refer to the proportion of the total sightings of each of the species.

Habitat type	***C. niloticus***	***M. leptorhynchus***	***O. tetraspis***	**Total**
Lagoon	33 (91.7%)	133 (45.9%)	5 (21.7%)	**171**
Lakes	0 (0.0%)	69 (23.8%)	8 (34.8%)	**77**
River	3 (8.3%)	88 (30.3%)	10 (43.5%)	**101**
Total	**36**	**290**	**23**	**349**

The numbers of encounters with small crocodiles (< 60 cm total body length) varied significantly between the three habitats ($\chi^2 = 35.246$, df = 4, $P < 0.001$). Small *C. niloticus* (53 ± 5 cm) were most frequent in the lagoon, and accounted for 60.0% of all *C. niloticus* encountered. Small *M. leptorhynchus* (52 ± 6 cm) and *O. tetraspis* (52 ± 4 cm) were less numerous, and were most frequent in the river, accounting for 12.3% and 17.4% of all respective species encounters (Fig. 3.6).

The distribution of medium-sized crocodiles (61–200 cm total body length) also significantly varied between the three main habitat types ($\chi^2 = 10.308$, df = 4, $P = 0.036$). Both medium *C. niloticus* (124 ± 45 cm) and *M. leptorhynchus* (115 ± 33 cm) were most frequent in the lagoon (25.7% of all *C. niloticus* and 39.8% of all *M. leptorhynchus* encounters), while medium *O. tetraspis* (96 ± 16 cm) were most frequent in the lakes (30.4% of all encounters) and the river (26.1% of all encounters). Individuals over 200 cm total body length were not frequently encountered in any of the habitat types.

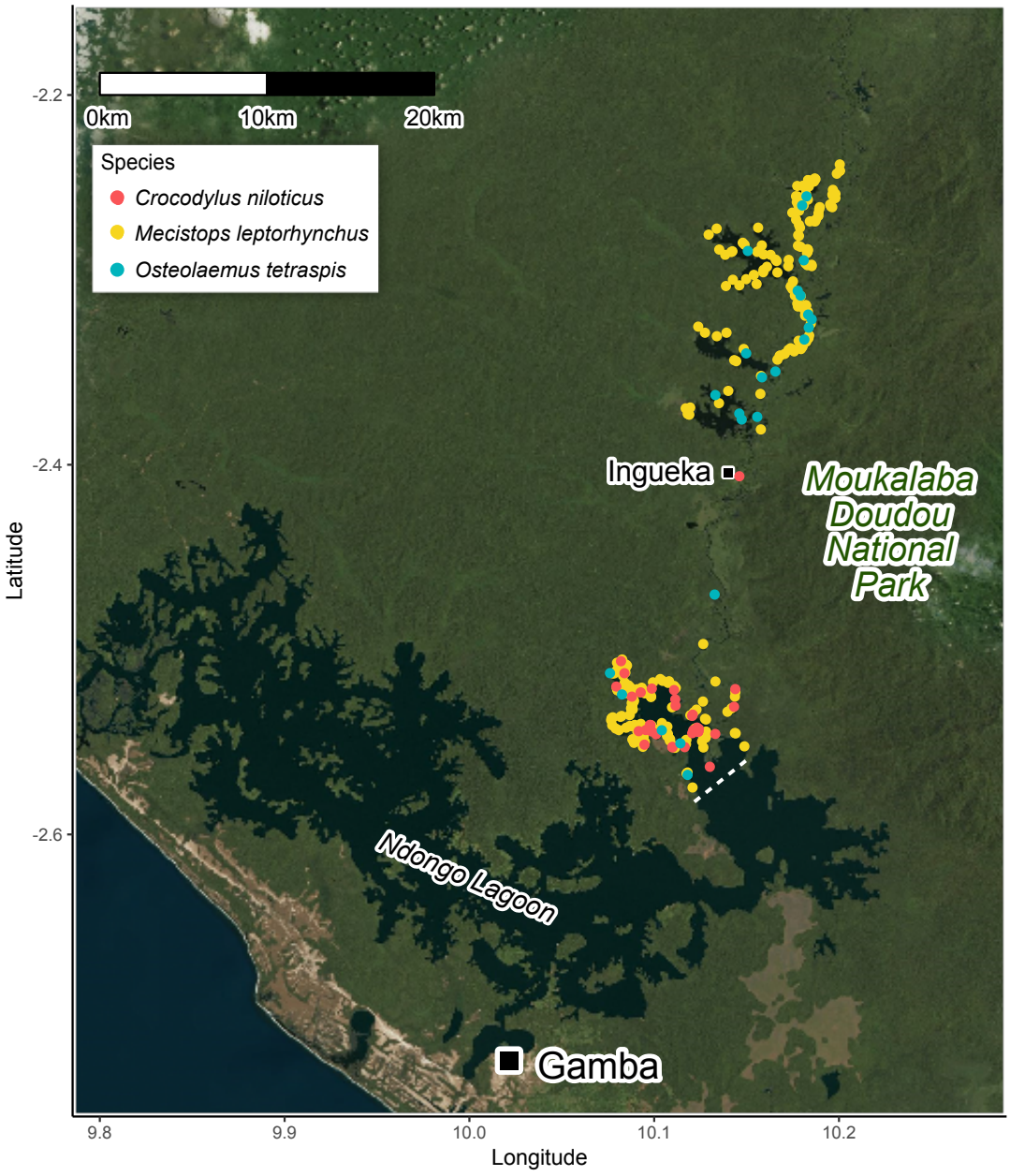

FIGURE 3.5. Locations of *C. niloticus*, *M. leptorhynchus* and *O. tetraspis* spotted in the Bongo River area (Gabon). White dashed line marks the limit of the section of the lagoon surveyed during the study. Base map: Bing Map Aerial.

Large *C. niloticus* (350 ± 71 cm) were found only in the lagoon and accounted for 5.7% of all *C. niloticus* encountered, while most large *M. leptorhynchus* (235 ± 20 cm) were found in the river (2.1% encountered of *M. leptorhynchus*, Fig. 3.6).

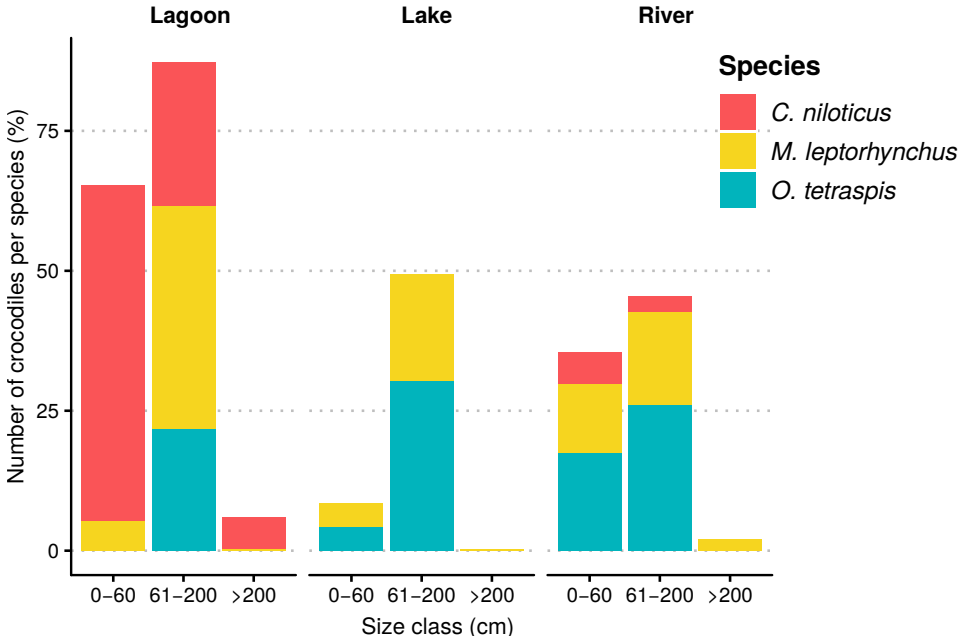

FIGURE 3.6. Percentage of the proportion of the total sightings of each crocodile species in the three habitat types of the Bongo River region (Gabon) divided into three size classes. Body length 0–60 cm: *C. niloticus* $n_{lagoon} = 21$, $n_{river} = 2$; *M. leptorhynchus* $n_{lagoon} = 15$, $n_{lake} = 12$, $n_{river} = 35$; *O. tetraspis* $n_{lake} = 1$, $n_{river} = 4$. Body length 61–200 cm: *C. niloticus* $n_{lagoon} = 9$, $n_{river} = 1$; *M. leptorhynchus* $n_{lagoon} = 113$, $n_{lake} = 54$, $n_{river} = 47$; *O. tetraspis* $n_{lagoon} = 5$, $n_{lake} = 7$, $n_{river} = 6$. Body length > 200 cm: *C. niloticus* $n_{lagoon} = 2$; *M. leptorhynchus* $n_{lagoon} = 1$, $n_{lake} = 1$, $n_{river} = 6$.

3.3.1.2 Crocodile habitat availability and habitat use

Lagoon. The model chosen by stepwise model selection as the minimum adequate model for microhabitats of the three crocodile species in the lagoon was a function of percentage vegetation cover, distance to shore, bank slope and shore habitat type ($\Delta\text{AIC}_{null} = 58.772$, $\chi^2 = 429$, df = $873, 15$, $P < 0.001$; Table 3.3). Regression coefficients showed that *C. niloticus* lagoon habitat selection was positively influenced by percentage of vegetation cover, the presence of grassland and papyrus, and negatively influence by bank slope. Habitat selection by *M. leptorhynchus* was positively influenced by percentage of vegetation cover, and negatively influenced by the presence of grassland shore. For *O. tetraspis*, habitat selection in the lagoon was negatively influenced by the distance to shore (Table 3.3).

There was a significant difference in the preferred distance to land (Kruskal-Wallis $\chi^2 =$

TABLE 3.3. Results of the multinomial logistic regression for lagoon (Gabon) microhabitat selection by *C. niloticus* ($n = 33$), *M. leptorhynchus* ($n = 133$) and *O. tetraspis* ($n = 5$). Shows coefficient for the constant (B), standard error (SE) and P-value (P). P-values of variables with significant effect ($P < 0.05$) are presented in bold. Habitat variables not used in the model are noted as "–". Very large standard error values resulting from low number of *O. tetraspis* sightings are noted as n/a.

Species	**Habitat parameters**	***B***	**SE**	***P***
C. niloticus	Intercept	-2.646	0.132	**0.008**
	Water level (m)	–	–	–
	Vegetation cover (%)	4.280	1.033	< **0.001**
	Distance to shore (m)	−0.740	0.964	0.459
	Distance to vegetation (m)	–	–	–
	Bank slope	−3.230	0.957	**0.001**
	Shore (grassland)	3.101	29.392	**0.002**
	Shore (palm)	−0.015	0.989	0.988
	Shore (papyrus)	2.050	5.173	**0.040**
M. leptorhynchus	Intercept	−1.370	0.132	0.171
	Water level (m)	–	–	–
	Vegetation cover (%)	6.310	1.036	< **0.001**
	Distance to shore (m)	−0.563	0.981	0.573
	Distance to vegetation (m)	–	–	–
	Bank slope	−1.255	0.993	0.210
	Shore (grassland)	−2.487	0.187	**0.013**
	Shore (palm)	−1.060	0.560	0.286
	Shore (papyrus)	−1.171	0.421	0.242
O. tetraspis	Intercept	987.207	n/a	< **0.001**
	Water level (m)	–	–	–
	Vegetation cover (%)	−0.477	0.277	0.633
	Distance to shore (m)	−4101.938	n/a	< **0.001**
	Distance to vegetation (m)	–	–	–
	Bank slope	−0.120	0.643	0.904
	Shore habitat	n/a	n/a	n/a

16.022, df = 2, $P < 0.001$) and the percentage of vegetation cover (Kruskal-Wallis $\chi^2 = 9.038$, df = 2, $P = 0.012$) between the three species in the lagoon (Fig. 3.8, 3.9). *Osteolaemus teraspis* was encountered in areas with higher vegetation cover ($99 \pm 2\%$) compared to *C. niloticus* ($59 \pm 36\%$) and *M. leptorhynchus* ($60 \pm 34\%$) and was predominantly found on land, away from the shore (-3.4 ± 0.9 m), while both *C. niloticus* and *M. leptorhynchus* were in the water, further away from the shore (*C. niloticus* = 9.3 ± 7.7 m; *M. leptorhynchus* = 7.3 ± 6.3 m). *Crocodylus niloticus* and *M. leptorhynchus* differed significantly in their preferred shore habitat in the lagoon ($\chi^2 = 42.192$, df = 3, $P < 0.001$), with 84% of *M. leptorhynchus* found near the forest, compared to a broader range of shore habitats preferred by *C. niloticus* (forest = 37%, grassland = 27%, Raffia palms = 12%, papyrus = 24%; Fig. 3.7). *Osteolaemus tetraspis* were only encountered in the forest. Bank slope preference was not significantly different between the three species (Kruskal-Wallis

$\chi^2 = 4.481$, df = 2, $P = 0.106$; Fig. 3.8, 3.10).

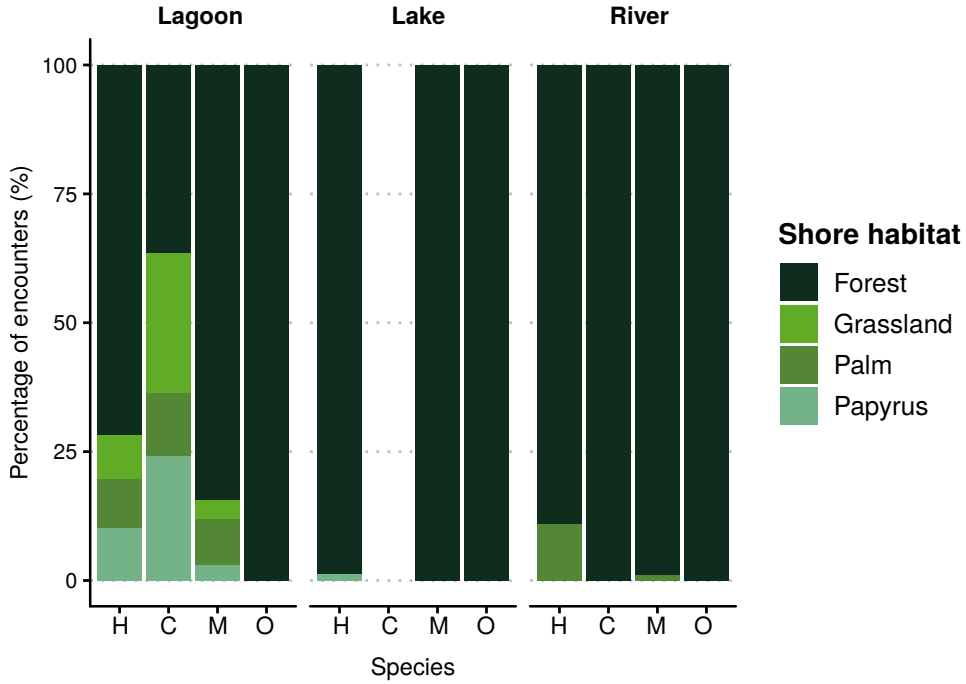

FIGURE 3.7. Percentage of shore habitat types in the lagoon, lakes and river (Gabon) recorded during habitat surveys (H) and at points where *C. niloticus* (C), *M. leptorhynchus* (M) and *O. tetraspis* (O) were encountered.

Lake. The model chosen by stepwise model selection as the minimum adequate model for microhabitat selection of *M. leptorhynchus* and *O. tetraspis* in the lake habitat was a function of water level, percentage of vegetation cover, distance to the nearest vegetation and bank slope ($\Delta\text{AIC}_{null} = 72.386$, $\chi^2 = 233$, df = 426,6, $P < 0.001$). Regression coefficients showed for both *M. leptorhynchus* and *O. tetraspis* the lake habitat selection was positively influenced by the percentage of vegetation cover, and negatively influenced by water level (Table 3.4). The distance to the nearest vegetation also had a significant positive influence on habitat selection for *M. leptorhynchus* (Table 3.4).

There was a significant difference in the preferred water level (Kruskal-Wallis $\chi^2 = 13.734$, df = 1, $P < 0.001$), and the associated distance to shore (Kruskal-Wallis $\chi^2 = 12.194$, df = 1, $P < 0.001$) between the *M. leptorhynchus* and *O. tetraspis* found the lakes (Fig. 3.8). *Osteolaemus tetraspis* were on or close to land (-0.6 ± 8.4 m), with shallow water (0.2 ± 0.5 m), while *M. leptorhynchus* were further away from land (12.9 ± 13.7 m), in deeper water (1.6 ± 0.9 m). The species did not differ significantly in their preferred percentage of vegetation cover (Kruskal-Wallis $\chi^2 = 0.857$, df = 1, $P = 0.354$), distance to nearest vegetation (Kruskal-Wallis $\chi^2 = 0.971$, df = 1, $P = 0.324$; Fig. 3.9) and bank slope (Kruskal-Wallis $\chi^2 = 0.260$, df = 1, $P = 0.612$; Fig. 3.10).

TABLE 3.4. Results of the multinomial logistic regression for lake (Gabon) microhabitat selection by *M. leptorhynchus* ($n = 69$) and *O. tetraspis* ($n = 8$). Shows coefficient for the constant (B), standard error (SE), and P-value (P). P-values of variables with significant effect ($P < 0.05$) are presented in bold. Habitat variables not used in the model are noted as "–".

Species	**Habitat parameters**	***B***	**SE**	***P***
M. leptorhynchus	Intercept	1.271	2.356	0.204
	Water level (m)	−5.050	0.181	< **0.001**
	Vegetation cover (%)	4.676	1.025	< **0.001**
	Distance to shore (m)	–	–	–
	Distance to vegetation (m)	3.284	1.091	**0.001**
	Bank slope	1.848	1.018	0.0646
	Shore habitat	–	–	–
O. tetraspis	Intercept	0.720	2.348	0.472
	Water level (m)	−4.687	0.012	< **0.001**
	Vegetation cover (%)	2.537	1.038	**0.011**
	Distance to shore (m)	–	–	–
	Distance to vegetation (m)	0.855	1.138	0.393
	Bank slope	−0.495	0.988	0.621
	Shore habitat	–	–	–

River. The model chosen by stepwise model selection as the minimum adequate model of microhabitat selection of *C. niloticus*, *M. leptorhynchus* and *O. tetraspis* in the river was the function of percentage vegetation cover and distance to shore ($\Delta\text{AIC}_{null} = 156.298$, $\chi^2 = 271$, df = $756,3$, $P < 0.001$). Regression coefficients showed that river habitat selection in all three species was negatively influenced by distance to shore (Table 3.5). For *M. leptorhynchus*, percentage of vegetation cover also had a significant negative effect on the habitat selection.

Between the three species encountered in the river, there were significant differences in preferred distance to shore (Kruskal-Wallis $\chi^2 = 14.459$, df = 2, $P < 0.001$) and the associated water level (Kruskal-Wallis $\chi^2 = 6.842$, df = 2, $P = 0.033$). *Osteolaemus tetraspis* were encountered on or close to land (-1.7 ± 1.7 m), with shallow water (0.5 ± 1.3 m), while *C. niloticus* and *M. leptorhynchus* were in deeper water (*C. niloticus*: 1.3 ± 1.5 m, *M. leptorhynchus*: 1.4 ± 1.6 m), away from land (*C. niloticus*: 0.9 ± 0.7 m, *M. leptorhynchus*: 0.7 ± 1.8 m) (Fig. 3.8). There were no significant differences in the preferred percentage vegetation cover (Kruskal-Wallis $\chi^2 = 2.453$, df = 2, $P = 0.293$), distance to the nearest vegetation (Kruskal-Wallis $\chi^2 = 0.308$, df = 2, $P = 0.857$; Fig. 3.9) and bank slope (Kruskal-Wallis $\chi^2 = 2.233$, df = 2, $P = 0.327$; Fig. 3.10).

3.3.2 South-western Taï National Park, Côte d'Ivoire

3.3.2.1 Species and size distribution of crocodiles

The south-western region of Taï National Park had two species of crocodiles present during the study period: *Mecistops cataphractus* and *Osteolaemus* aff. *tetraspis* (Fig. 3.11). *Mecistops*

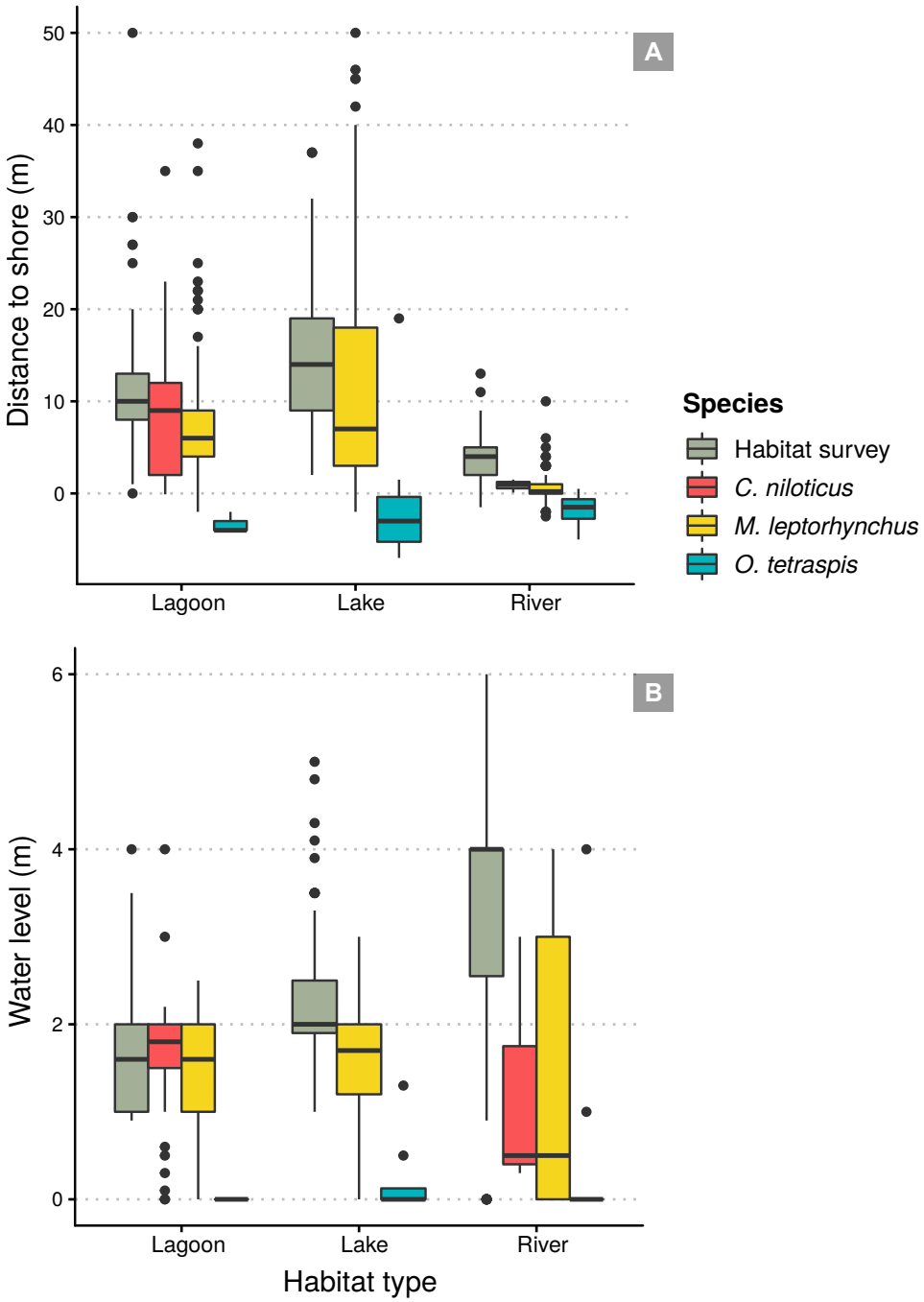

FIGURE 3.8. Distance to shore (A) and water level (B) in the lagoon, lakes and river (Gabon), measured during habitat surveys and points where *C. niloticus*, *M. leptorhynchus* and *O. tetraspis* were encountered. The boxes depict 25th percentiles, median line and 75th percentiles of the measured values, and the whiskers represent 95% confidence intervals. Dots represent outliers.

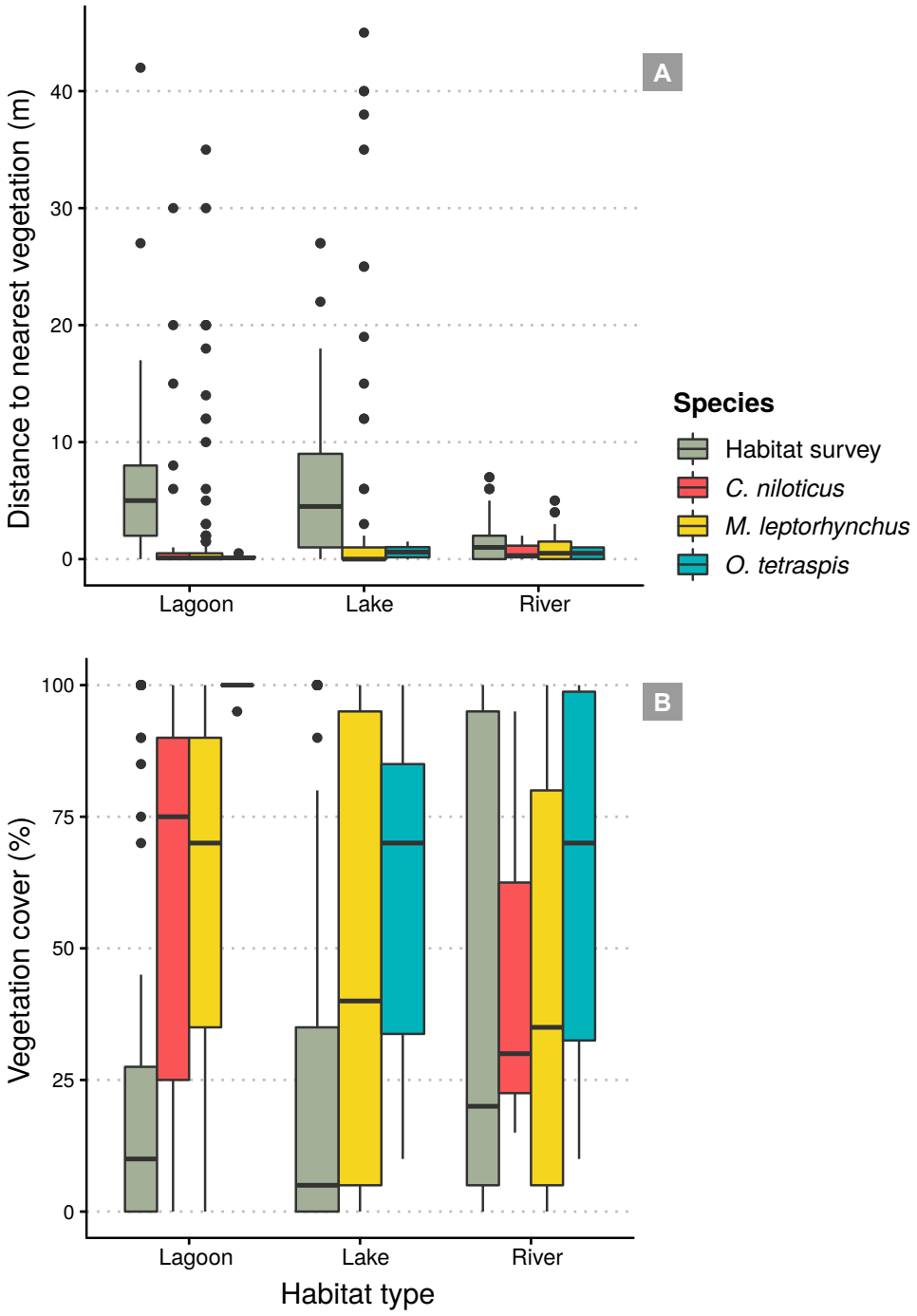

FIGURE 3.9. Distance to the nearest vegetation (A) and the percentage of vegetation cover (B) in the lagoon, lakes and river (Gabon), measured during habitat surveys and points where *C. niloticus*, *M. leptorhynchus* and *O. tetraspis* were encountered. The boxes depict 25th percentiles, median line and 75th percentiles of the measured values, and the whiskers represent 95% confidence intervals. Dots represent outliers.

TABLE 3.5. Results of the multinomial logistic regression for river (Gabon) microhabitat selection by *C. niloticus* ($n = 3$), *M. leptorhynchus* ($n = 88$) and *O. tetraspis* ($n = 10$). Shows coefficient for the constant (B), standard error (SE) and P-value (P). P-values of variables with significant effect ($P < 0.05$) are presented in bold. Habitat variables not used in the model are noted as "–".

Species	**Habitat parameters**	***B***	**SE**	***P***
C. niloticus	Intercept	−1.056	0.315	0.291
	Water level (m)	–	–	–
	Vegetation cover (%)	−1.240	0.981	0.215
	Distance to shore (m)	−2.307	0.412	**0.021**
	Distance to vegetation (m)	–	–	–
	Bank slope	–	–	–
	Shore habitat	–	–	–
M. leptorhynchus	Intercept	5.401	11.474	< **0.001**
	Water level (m)	–	–	–
	Vegetation cover (%)	−4.363	0.978	< **0.001**
	Distance to shore (m)	−7.869	0.373	< **0.001**
	Distance to vegetation (m)	–	–	–
	Bank slope	–	–	–
	Shore habitat	–	–	–
O. tetraspis	Intercept	−1.142	0.310	0.254
	Water level (m)	–	–	–
	Vegetation cover (%)	−0.726	0.992	0.468
	Distance to shore (m)	−5.913	0.103	< **0.001**
	Distance to vegetation (m)	–	–	–
	Bank slope	–	–	–
	Shore habitat	–	–	–

cataphractus was the most common species encountered, accounting for 125 of the total 130 confirmed species sightings (Table 3.6). *Osteolaemus* aff. *tetraspis* was encountered five times in total, both in and outside of the protected area (Table 3.6).

TABLE 3.6. Numbers of crocodile sightings confirmed to species on the Hana River (Côte d'Ivoire) inside the south-western Taï National Park, the park border and the cocoa plantation area. Percentages refer to the proportion of the total sightings of each of the species.

Habitat type	***M. cataphractus***	***O. tetraspis***	**Total**
Plantation	21 (16.8%)	2 (40.0%)	**23**
Border	79 (63.2%)	2 (40.0%)	**81**
Taï National Park	25 (20.0%)	1 (20.0%)	**26**
Total	**125**	**5**	**130**

Medium *M. cataphractus* (108 ± 4 cm) were the most common size class encountered, accounting for 68% of all *M. cataphractus*, while small (55 ± 5 cm) and large (251 ± 29 cm) individuals

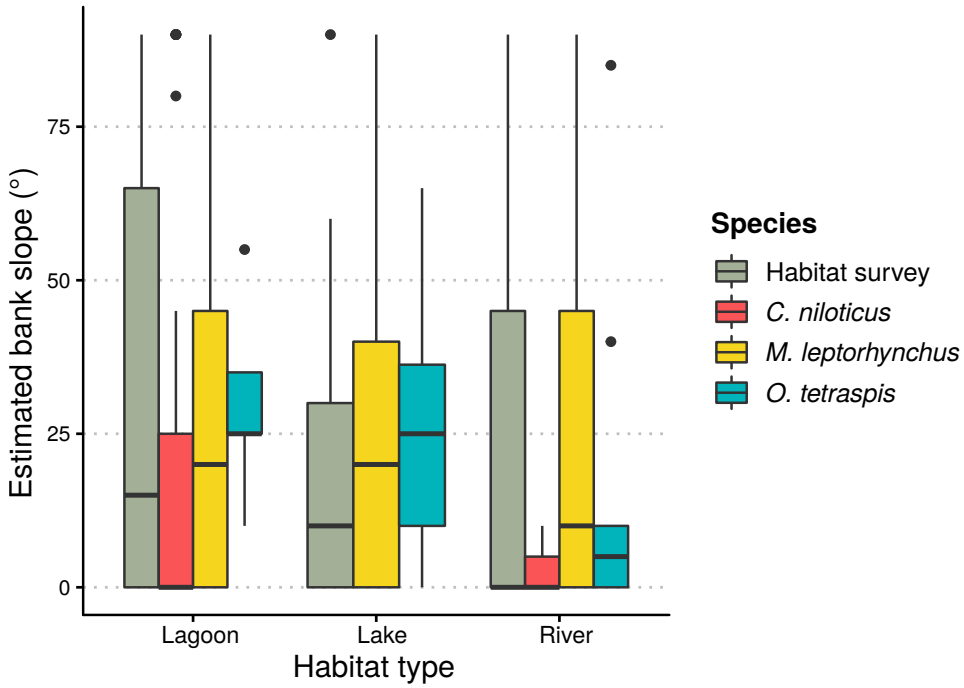

FIGURE 3.10. Estimated bank slope in the lagoon, lakes and river (Gabon) measured during habitat surveys and points where *C. niloticus*, *M. leptorhynchus* and *O. tetraspis* were encountered. The boxes depict 25th percentiles, median line and 75th percentiles of the slope, and the whiskers represent 95% confidence intervals. Dots represent outliers.

accounted for 19.2% and 12.8% respectively (Fig. 3.12). Only medium *O.* aff. *tetraspis* (98 ± 4 cm) were encountered during the study period. Small and medium-sized *M. cataphractus* were found significantly more frequently at the park border than the Taï National Park interior or plantation area (small *M. cataphractus*: $\chi^2 = 21$, df = 2, $P < 0.001$; medium *M. cataphractus*: $\chi^2 = 39.977$, df = 2, $P < 0.001$). There was no significant difference in the frequency of encounters of large *M. cataphractus* between the three areas ($\chi^2 = 2.923$, df = 2, $P = 0.232$).

3.3.2.2 Crocodile habitat availability and habitat use

The model chosen by stepwise model selection as the minimum adequate model of microhabitat selection in the Hana and Meno rivers was the function of water level, percentage vegetation cover, distance to shore and bank slope (ΔAIC = 53.817, $\chi^2 = 296$, df = 484,6, $P < 0.001$; Table 3.7). Regression coefficients showed that habitat selection in *M. cataphractus* was negatively influenced by distance to shore and water level, and positively influenced by bank slope the percentage of vegetation cover (Table 3.7).

There was a significant difference in the preferred percentage vegetation cover (Mann-Whitney $W = 151.5$, $n_1 = 125$, $n_2 = 5$, $P = 0.040$), distance to shore (Mann-Whitney $W = 636.5$,

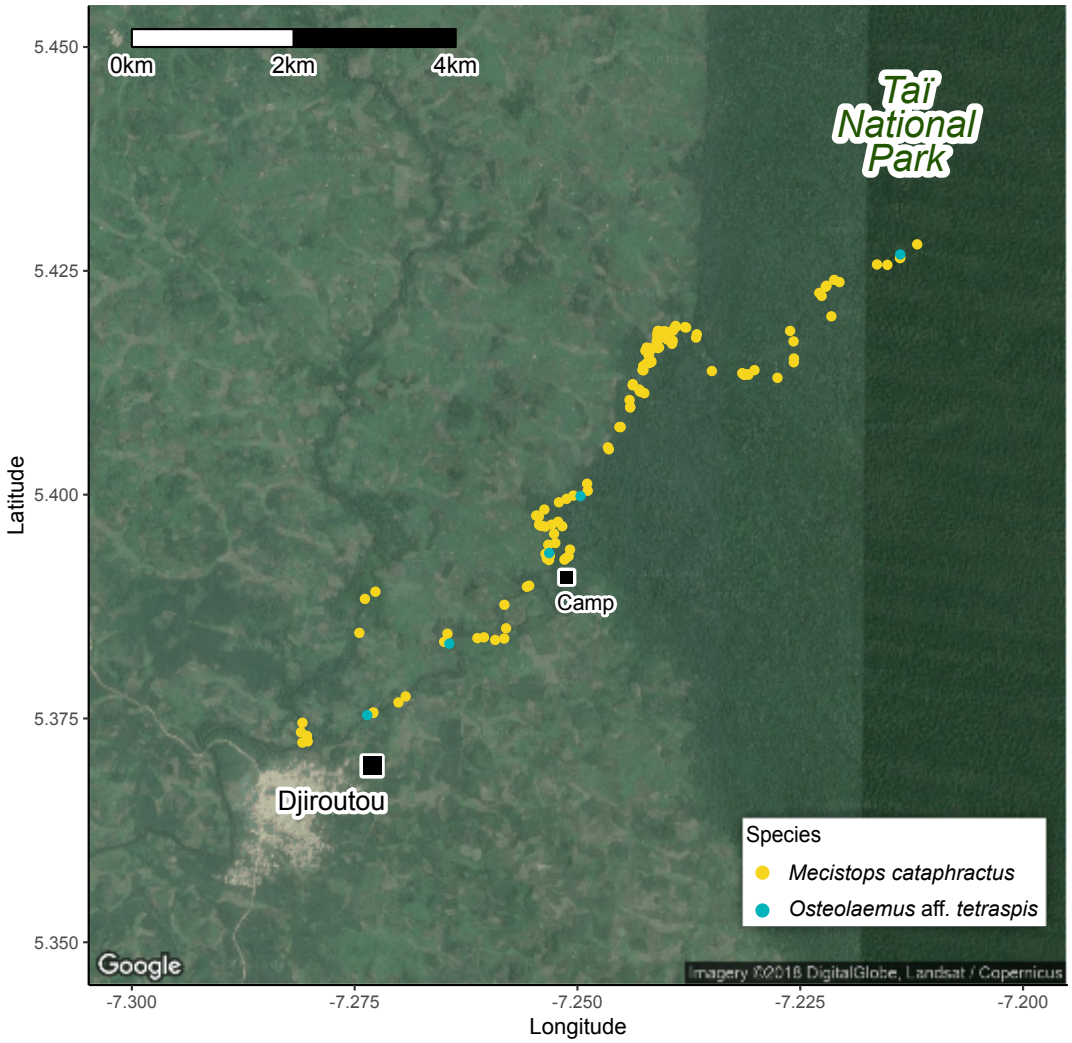

FIGURE 3.11. Locations of *M. cataphractus* and *O.* aff. *tetraspis* spotted in the Hana and Meno rivers in Taï National Park (Côte d'Ivoire). Base map: Google Satellite.

$n_1 = 125$, $n_2 = 5$, $P < 0.001$) and the associated water level (Mann-Whitney $W = 613$, $n_1 = 125$, $n_2 = 5$, $P = 0.001$) between *M. cataphractus* and *O. tetraspis* (Fig. 3.13). *Osteolaemus* aff. *tetraspis* were found on or close to land (-5.8 ± 5.8 m), with shallow water (0.1 ± 0.3 m) and large vegetation cover ($77 \pm 26\%$), while *M. cataphractus* were in deeper water (1.1 ± 1.0 m) further away from land (2.9 ± 3.7 m), and with less vegetation cover ($43 \pm 36\%$). The species did not differ significantly in their preferred bank slope (Mann-Whitney $W = 470.5$, $n_1 = 125$, $n_2 = 5$, $P = 0.105$) and distance to the nearest vegetation (Mann-Whitney $W = 345.5$, $n_1 = 125$, $n_2 = 5$, $P = 0.862$; Fig. 3.14). *Mecistops cataphractus* found along the different sections of the rivers did not significantly differ in any of the parameters measured (see Appendix A, Table A.2).

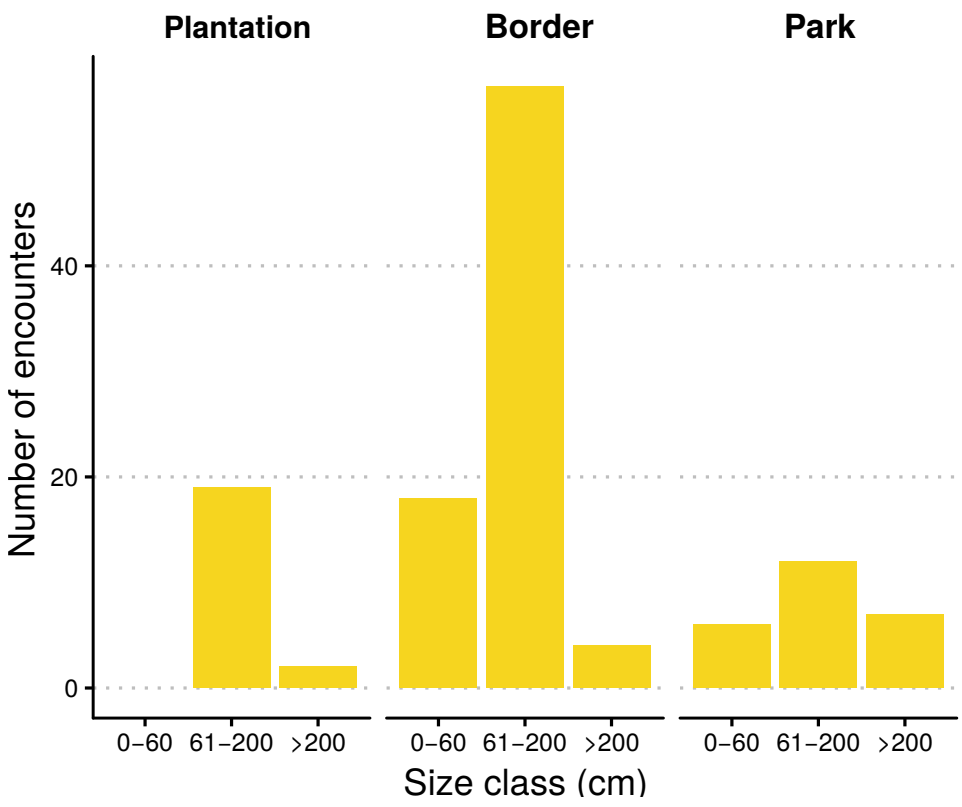

FIGURE 3.12. Percentage of *M. cataphractus* encountered in Côte d'Ivoire in the Taï National Park interior, divided into three size classes by habitat type (park edge, outside of protected area, in cocoa plantation): (i) 0–60 cm body length ($n_{plantation} = 0$, $n_{border} = 18$, $n_{park} = 6$); (ii) 61–200 cm body length ($n_{plantation} = 19$, $n_{border} = 57$, $n_{park} = 12$); and (iii) > 200 cm body length ($n_{plantation} = 2$, $n_{border} = 4$, $n_{park} = 7$).

3.4 Discussion

Habitat partitioning was observed between the sympatric crocodilians in both study sites. In the Bongo River region of Gabon, the species differed in preferences both between the lagoon, lakes and river, as well as within each of the three main habitat types. *Mecistops leptorhynchus* and *O. tetraspis* were found in all three areas, while *C. niloticus* was only present in the lagoon and river. In the south-western Taï National Park area, *M. cataphractus* and *O.* aff. *tetraspis* were found along both protected and unprotected areas of the Hana River, but the species differed in habitat parameter preferences.

In the Bongo River region, *Mecistops leptorhynchus* was the most commonly encountered crocodilian. While some individuals were found in the open waters of the lagoon and the lakes, the species preferred vegetation cover in all three habitat types, and was predominantly found in the shallow water near forested banks. In the lagoon, where it was sympatric with *C. niloticus*, *M. leptorhynchus* was less likely to be found near the grassland shores, while the Nile crocodiles

TABLE 3.7. Results of the multinomial logistic regression for microhabitat selection by *M. cataphractus* ($n = 125$) and *O. tetraspis* ($n = 5$) in the rivers in south-western region of Taï National Park, Côte d'Ivoire. Shows coefficient for the constant (B), standard error (SE) and P-value. P-values of variables with significant effect ($P < 0.05$) are presented in bold. Habitat variables not used in the model are noted as "–".

Species	**Habitat parameters**	***B***	**SE**	***P***
M. cataphractus	Intercept	−0.751	0.750	0.453
	Water level (m)	−2.867	0.598	**0.004**
	Vegetation cover (%)	4.022	1.020	< **0.001**
	Distance to shore (m)	-3.700	0.862	< **0.001**
	Distance to vegetation (m)	–	–	–
	Bank slope	2.962	1.017	**0.003**
	Vegetation type	–	–	–
O. tetraspis	Intercept	−0.541	0.289	0.589
	Water level (m)	0.060	1.195	0.953
	Vegetation cover (%)	0.945	1.030	0.344
	Distance to shore (m)	−1.642	0.076	0.101
	Distance to vegetation (m)	–	–	–
	Bank slope	−0.843	0.945	0.339
	Vegetation type	–	–	–

preferred the areas near grassland and papyrus with flatter banks and greater vegetation cover. *Osteolaemus tetraspis* was rarely encountered in all three habitat types, and was always found in the forest, on or close to land.

These results are concordant with earlier reports on habitat preferences in *M. leptorhynchus* and *O. tetraspis* (Waitkuwait, 1989; Eaton, 2010; Shirley et al., 2018). Slender-snouted crocodiles generally inhabit continuous aquatic habitats, primarily in forested lakes and larger rivers (Shirley et al., 2018), while dwarf crocodiles are considered more terrestrial (Shirley and Austin, 2017), occupying small streams and swamps in the forest, often further away from the larger waterways (Waitkuwait, 1989; Eaton, 2010).

Nile crocodiles are habitat generalists with a broad distribution range across East and Southern Africa, but their distribution in Gabon is confined to coastal lagoons (Trutnau and Sommerlad, 2006; Isberg et al., 2019). The majority of *C. niloticus* encountered in the northern Ndongo Lagoon were small individuals. Unlike *M. leptorhynchus* and *O. tetraspis* that build mound nests in the forest during the rainy season (Waitkuwait, 1989), *C. niloticus* breeds in the dry season, digging nest holes in sandy banks (Fergusson, 2010). The lagoon provided suitable nesting habitat for *C. niloticus*, and their nests have been found in previous seasons in the grassland area (Tobi Eli, pers. comm.). The small Nile crocodiles encountered in the lagoon were thus likely the hatchlings, as well as possible yearlings from the previous season.

In many species of animal, different habitats are used by individuals at different life stages (Halpern et al., 2005). Crocodilians also experience ontogenetic niche shifts throughout their

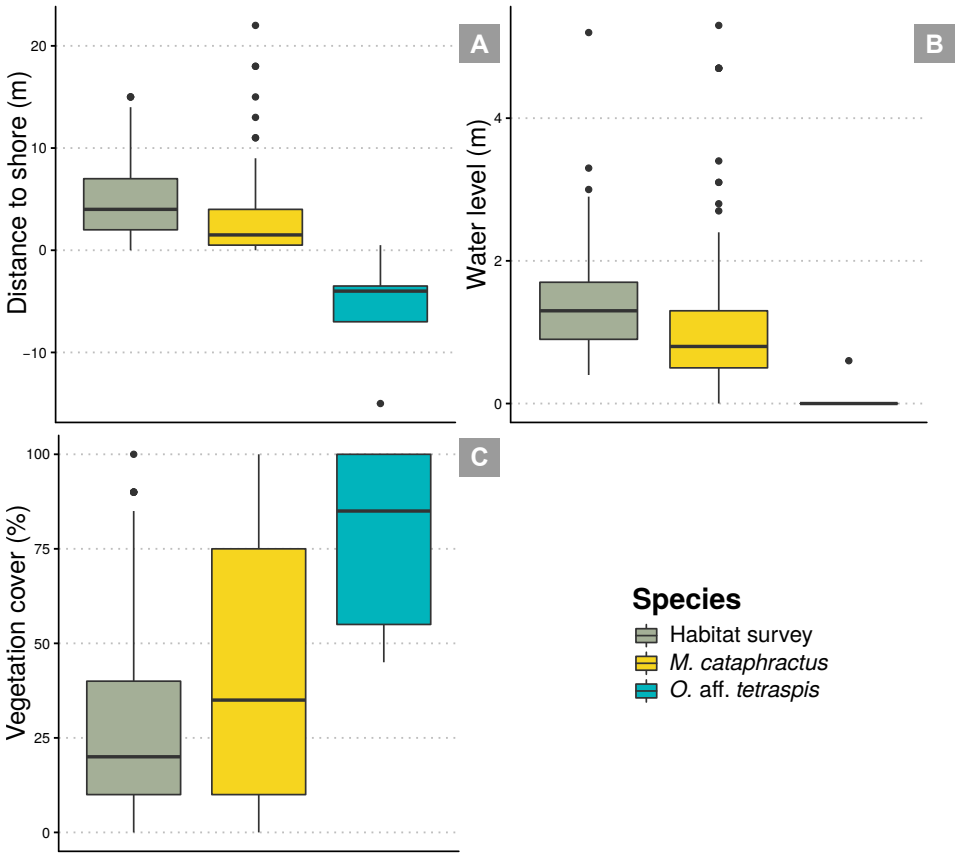

FIGURE 3.13. Distance to shore (A), water level (B), and the percentage vegetation cover (C) in Hana and Meno rivers (Côte d'Ivoire) measured during habitat surveys and points where *M. cataphractus* and *O.* aff. *tetraspis* were encountered. The boxes depict 25th percentiles, median line, and 75th percentiles of the measured values, and the whiskers represent 95% confidence intervals. Dots represent outliers.

lives, as their environmental requirements for shelter, food, basking or nesting sites change (Ouboter, 1996b; Subalusky et al., 2009; Somaweera et al., 2018). The increased percentage of vegetation cover, including the papyrus preferred by *C. niloticus* encountered in the lagoon, could provide shelter from predators, including other crocodiles. Medium and large *C. niloticus* were also present in the lagoon, but they were found in smaller numbers. Size-class separation in *C. niloticus* has previously been linked to cannibalism and predator avoidance (Hutton, 1989). While the home ranges of adult females tend to be close to the nesting sites, enabling them to assist and protect the hatchlings (Pooley, 1977; Chabert et al., 2015), medium-sized juveniles and sub-adult *C. niloticus* disperse to avoid conflict with the adults (Hutton, 1989), and Trutnau and Sommerlad (2006) noted that medium *C. niloticus* are generally less commonly encountered in the wild. In the Bongo River region, adult *C. niloticus* were only encountered in the lagoon. Crocodilians become more wary with age (Ron et al., 1998), often making large animals difficult to approach and identify, particularly in areas affected by hunting (Thibault and Blaney, 2003;

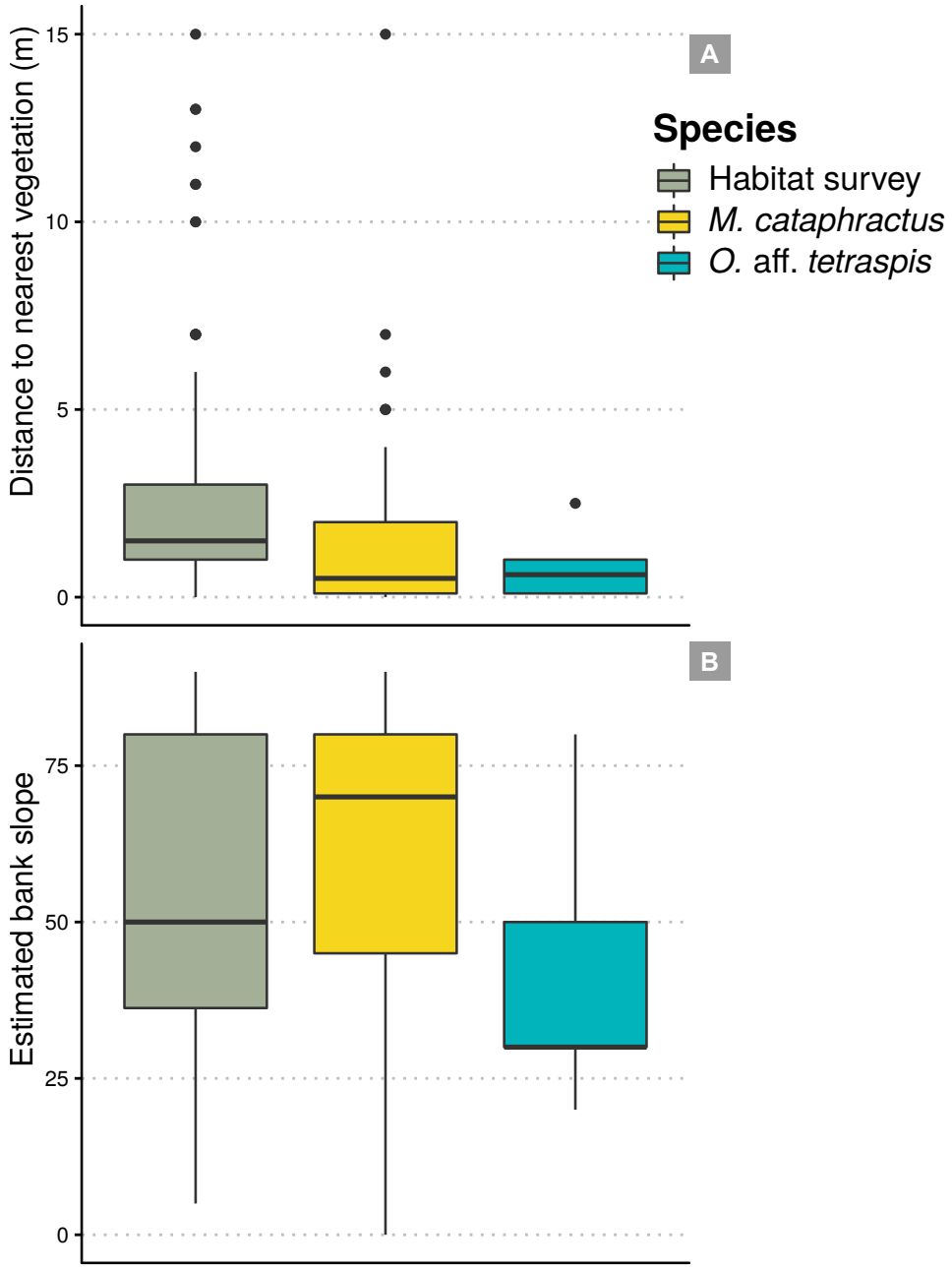

FIGURE 3.14. Distance to nearest vegetation (A) and bank slope (B) in Hana and Meno rivers (Côte d'Ivoire) measured during habitat surveys and points where *M. cataphractus* and *O.* aff. *tetraspis* were encountered. The boxes depict 25th percentiles, median line, and 75th percentiles of the measured values, and the whiskers represent 95% confidence intervals. Dots represent outliers.

Isberg et al., 2019), thus it is possible that large *C. niloticus* were also present in the other habitat types. However, the presence of suitable *C. niloticus* nesting sites in the lagoon, as well as possible competition with the sympatric *M. leptorhynchus*, could be limiting the adult presence to this one habitat type.

Slender-snouted and dwarf crocodiles were encountered in all three habitat types, but their size-class distribution was different to that of *C. niloticus*. As the species are thought to nest during the rainy season (Waitkuwait, 1989; Shirley et al., 2018), hatchlings had not yet emerged at the time of the surveys, and although small *M. leptorhynchus* and *O. tetraspis* were encountered, they were more common in the river and the lakes than in the lagoon. Hatchling and juvenile crocodilians suffer high mortality rates (Hussain, 1999; Webb et al., 1983a; Somaweera et al., 2013). Large *C. niloticus* pose a threat to other smaller crocodilians, thus the low numbers of small *M. leptorhynchus* and *O. tetraspis* in the lagoon could be a result of predator avoidance. While little is known about the home range size and ontogenetic shifts in habitat requirements in *M. leptorhynchus*, the species build mound nests under closed canopy forests and the breeding requirements likely limit their distribution to heavily forested rivers and lakes (Shirley et al., 2018). Although large *M. leptorhynchus* were rarely encountered in the Bongo River region, the majority of encounters occurred in the river, where suitable nesting habitat could be found.

Although the large number of encounters of *M. leptorhynchus* in the study area indicates the area remains a stronghold for this Critically Endangered species, the large proportion of medium (60–200 cm) *M. leptorhynchus* across all habitats should not be viewed as a direct measure of the population structure. The combination of repeated sampling method and the exclusion of all unidentified crocodiles encountered during the surveys, as well as increased difficulty in approaching and identifying large individuals, likely resulted in a skewed proportion of size classes. While the possible repeated encounters with the same individuals on different nights were not excluded in the analysis, as each represented an independent habitat parameter preference choice for the species, juvenile crocodiles are more likely to be successfully approached and identified, and are more likely to be approached repeatedly (Ron et al., 1998; Staniewicz et al., 2018). Shirley et al. (2018) estimated the general size class structure of the *M. leptorhynchus* surveyed across the species range to be composed of 53% hatchlings/small juveniles, 32% juveniles/subadults, and 7% adults. However, 46% of encountered crocodiles were unidentified (Shirley et al., 2018), suggesting that these proportions also remain inaccurate, and indicating a need for monitoring methods that better target adult individuals and allow for better size-class identification.

In the rivers of the south-western Taï National Park area, Côte d'Ivoire, *M. cataphractus* was the most frequently encountered species, with *O.* aff. *tetraspis* accounting for 3.8% of all encounters. These results are in accordance with observations by Waitkuwait (1989), who recorded the crocodile populations on Hana River in 1986 to consist of 4.5% *Osteolaemus* sp. and 95.5% *Mecistops* sp.

Habitat preferences of the *M. cataphractus* and *O.* aff. *tetraspis* in the Hana and Meno

Rivers were similar to those of *M. leptorhynchus* and *O. tetraspis* found in Bongo River of Gabon. Compared to the habitat available in the Hana and Meno rivers, *M. cataphractus* preferred shallow waters close to the shore, with greater vegetation cover and steeper banks. Small and medium *M. cataphractus* were more frequently encountered in the protected region of the Hana River (the Taï National Park interior and the park border), than outside of the protected zone, in the plantation area. Bushmeat hunting, as well as incidental deaths in fishing nets remain among the main threats to *M. cataphractus* in the wild (Shirley, 2014). Fishing and hunting are prohibited both inside Taï National Park and in the river along the border of the park, thus higher numbers of encounters with *M. cataphractus* in the protected area are to be expected. However, as in Gabon, the proportion of medium-sized *M. cataphractus* encountered in the study may be inflated due to repeated surveys and the easier boat transition along the park border, compared to that inside the park and along the plantations, where fallen trees and rapids increased the difficulty of successfully approaching and identifying crocodiles. As poaching still occurs in the area (pers. obs.), further studies are needed to determine whether the proximity to human settlements significantly affects the crocodile density, as seen in crocodilians in other areas (Shaney et al., 2017).

Osteolaemus aff. *tetraspis* was primarily found on land, in the forest with dense vegetation cover, and while the small sample size prevents from drawing definite conclusions on the habitat parameters selected by the species, the results are consistent with previous reports on *Osteolaemus* spp. ecology (Waitkuwait, 1989; Eaton, 2010).

While *M. cataphractus* and *O.* aff. *tetraspis* were not sympatric with *Crocodylus* spp. in the study area, in areas where their ranges overlap with *Crocodylus suchus*, habitat partitioning has been reported. In Liberia, *C. suchus* were found in coastal lagoons and brackish water habitats, while *M. cataphractus* and *O.* aff. *tetraspis* inhabited water bodies and rivers further inland (Kofron, 1992). In Côte d'Ivoire and Ghana, *C. suchus* has been reported in lagoons and coastal rivers, as well as northern savannah woodland rivers, and *M. cataphractus* were found primarily in the forested rivers in the southern parts of the countries (Shirley et al., 2009).

The distribution of the sympatric species in both study sites indicated habitat partitioning within the sympatric species groups, with preferences possibly related to breeding habitat, although adult animals were rarely encountered in both countries. In both regions, I conducted the surveys only during the rainy season, in order to coincide with higher acoustic activity of *Mecistops* and *Osteolaemus* associated with their courtship and mating. Possible seasonal variation in habitat preferences, as well as ontogenetic shifts in habitat of *C. niloticus*, *Mecistops* and *Osteolaemus* spp. require further studies.

All crocodile surveys presented here were conducted from motorised boats, and due to constraints, smaller streams in the forest interior were not sampled. As dwarf crocodiles have been reported in the study areas during previous surveys in the Gamba Complex and Taï National Park (Waitkuwait, 1989; Pauwels et al., 2006a; Shirley, 2010b), the low numbers found here

are likely an indication of habitat partitioning, rather than small population size (Shirley et al., 2009). This has important implications for crocodilian monitoring projects targetting sympatric *Mecistops* spp. and *Osteolaemus* spp. concurrently, as methods suitable for detecting one of the species may not be so for the other.

While the practical difficulties in finding and monitoring *Osteolaemus* spp. prevent estimating the current population density and numbers (Shirley, 2010b), methods such as acoustic monitoring deployed inside the forest areas, could provide more information, particularly for the adult breeding population. In Chapter 4, I present the acoustic repertoire of adult *O. tetraspis*, providing a call database for future monitoring use.

CHAPTER 4

THE VOCAL REPERTOIRE IN ADULT AFRICAN DWARF CROCODILES

Abstract

Vocal communication in adult crocodilians is diverse and plays an important role during courtship, mating and territory defence. Adults produce a range of acoustic signals, including bellows/roars, infrasound pulses and head slaps, which are considered the universal behavioural repertoire in crocodilian communication. While the acoustic repertoires of several species of *Alligator* and *Crocodylus* have been relatively well documented, little is known about the acoustic communication in other crocodylid genera such as *Mecistops* and *Osteolaemus*. Here, I used passive acoustic recorders to capture 97 spontaneous vocal signals of a pair of captive adult *Osteolaemus tetraspis* and catalogue their acoustic repertoire. I compared the calls recorded in captivity with 201 suspected wild *O. tetraspis* calls recorded in Gabon, in order to determine whether the wild calls belong to the same species. Captive and wild crocodiles produced the same four types of calls, not previously identified in other crocodylids. Short, low-frequency "drums" (31 ± 12 Hz) were the most common, accounting for over half of both captive and wild vocalisations. Longer, low-frequency "rumbles" (40 ± 14 Hz) accounted for 25% of all calls, while two higher frequency sounds—"moos" (299 ± 133 Hz) and "gusts" (219 ± 108 Hz)—were relatively uncommon. The moos recorded in captivity and in the wild did not differ in any of the eight acoustic parameters measured, while the remaining three call types differed in 3–5 parameters. As acoustic parameters vary between the calls of different individuals, all wild vocalisations were most likely produced by *O. tetraspis*. The calls were mainly emitted during the night (93% of captive and 81% of wild calls), and did not appear to be associated exclusively with courtship and mating. While further research is needed to determine the function of the different call types in *O. tetraspis*, the results presented here can provide reference for species identification during acoustic monitoring.

4.1 Introduction

Crocodilians communicate using a variety of signals. In short-distance interactions, they often use visual and olfactory cues such as snout lifting, inflated posture or mandibular musk-gland excretions (Vliet, 1989; Grigg and Kirshner, 2015), and acoustic signals can also be used (Vliet, 1989; Setner, 2008). Long-distance communication relies mainly on loud acoustic calls propagating through the water and air, but if the crocodiles can see each other, visual signals may also be employed (Dinets, 2013b; Grigg and Kirshner, 2015).

Acoustic communication is used through all stages of the animals' lives (Vergne et al., 2009), but in adults it is particularly common during courtship, territory defence and parent-offspring interactions (Vergne et al., 2009; Dinets, 2013b). *Alligator* is considered the most vocal genus (Thorbjarnarson and Wang, 2010; Grigg and Kirshner, 2015). For example, diverse adult crocodilian vocal and non-vocal acoustic signals have been classified through studies on *Alligator mississippiensis* and *Alligator sinensis* (Garrick et al., 1978; Vliet, 1989; Wang et al., 2007; Reber et al., 2015).

The loud vocalisations produced by crocodilians are called "bellows" if emitted by alligatorids, and "roars" if by crocodylids (Garrick and Lang, 1977). Bellows are usually produced in the water from the "head-oblique-tail-arched" (HOTA) position (Vliet, 1989). Both male and female alligators produce bellows (Garrick and Lang, 1977) and bellowing has been reported as contagious (Vliet, 1989), with repeated bellow cycles, called bouts, spreading between alligators and creating choruses (Garrick et al., 1978). Male bellows are usually louder than those produced by females, and often include an infrasound component called sub-audible vibrations (SAVs) just before the audible bellow (Vliet, 1989). The dominant frequencies, containing most of the sound energy of *A. mississippiensis* bellows, are between 20–250 Hz in air and 20–100 Hz in water (Todd, 2007). The bellows can be detected over a larger distance in the water than in the air (Todd, 2007) and are suitable for long-distance signalling. Although experimental studies on the functions of roars and bellows are still lacking, they are thought to be assertive signals of dominance, aggression or territoriality and have been suggested to play a role in mate attraction (Grigg and Kirshner, 2015). "Hisses", which are extended audible exhalations, are the second type of vocal signal produced by crocodilians. They are composed of broad-spectrum, low-frequency (below 1 kHz) sound (Garrick et al., 1978) and often occur on land, particularly in response to intruders (Neill, 1971; Garrick et al., 1978).

Non-vocal acoustic signals include SAVs, narial geysering, head slaps, and jaw claps. The SAVs are partly below the range of human hearing, at about 20–30 Hz (Todd, 2007), and can be detected through the appearance of a "water dance" created by Faraday waves (Grigg and Kirshner, 2015). All crocodilian species have been observed producing infrasound calls (Dinets, 2013b; Jailabdeen et al., 2018). The functions, as well as production of the SAVs are not clear; Todd (2007) has suggested that they may be produced through rapid muscle contractions similar to some species of fish (Knight and Ladich, 2014). Narial geysering, which is rarely observed,

involves releasing the air from the external nares, which results in a stream of water being shot up 10–20 m in height (Garrick et al., 1978). Head slaps in *A. mississippiensis* are produced from the HOTA position (Vliet, 1989). The head is raised above the water surface leaving the lower jaw submerged, and then rapidly slapped down, splashing the water and clapping the jaws together (Garrick et al., 1978). Jaw claps have been described as rapid snapping of jaws at the surface to produce a loud "pop" but have been categorised as part of the head slapping behaviour in some studies (Dinets, 2013b; Grigg and Kirshner, 2015). Head slapping is an assertion display, with Vliet (1989) suggesting this may be involved in establishing and maintaining the dominance hierarchy.

The behaviour associated with acoustic signalling is conserved between and within species, and is likely to be similar to dinosaur behaviour (Setner, 2008; Brazaitis and Watanabe, 2011). However, the frequency of use of acoustic signals varies between species and between habitats (Dinets, 2013b). Head slaps are more commonly used by species living in continuous aquatic habitats, while vocal signals are used more frequently by species found in fragmented aquatic habitats (Dinets, 2011). *Alligator sinensis*, which lives in heavily vegetated wetlands, has been reported to have a large vocal repertoire, which in addition to bellows, comprises "tooting", bubble blowing, "mooing", head slapping and "whining" (Wang et al., 2007). Bellowing is also very common in both species of *Alligator*, particularly at dawn and during courtship (Grigg and Kirshner, 2015). In contrast, in all members of Crocodylidae roaring is much less common (Grigg and Kirshner, 2015), though the acoustic signal composition can be variable between closely related species according to the habitat type they occupy (Dinets, 2013b). Vocal communication is both important and diverse in crocodilians. While the acoustic repertoire has been characterised for *Alligator* spp., as well as a number of *Crocodylus* spp., communication in other members of Crocodylidae has been largely ignored.

African dwarf crocodiles, *Osteolaemus*, are diminutive crocodilians, with adults reaching 1.8 m total body length (Waitkuwait, 1989). They are endemic to Central and West Africa, from the Democratic Republic of Congo to the Gambia (Eaton, 2010). Recent molecular and morphological studies confirmed the presence of at least three species within *Osteolaemus*: *O. tetraspis* inhabiting the Ogooué basin, *O. osbornii* in the Congo basin, and *O.* aff. *tetraspis* in West Africa (Fig. 2.7; Eaton et al., 2009; Shirley et al., 2014; Smolensky et al., 2015). Although the genus—previously listed and assessed as *O. tetraspis*—is considered widespread and locally abundant in many parts of their range and are classified as Vulnerable in the IUCN Red List of Threatened Species (Crocodile Specialist Group, 1996), limited surveys combined with bushmeat trade and habitat loss result in little information on their current population status (Eaton, 2010). *Osteolaemus* are reported to be highly terrestrial, often found in small forest streams and swamps away from large water bodies (Waitkuwait, 1989; Eaton, 2010; Shirley and Austin, 2017). They are mostly nocturnal, and hide in burrows or small pools during the day (Eaton, 2010). Except for a few recent studies (Pauwels et al., 2007; Eaton, 2010; Shirley et al., 2016), very

little is known about the basic ecology and behaviour of *O. tetraspis* in the wild. Their acoustic communication and vocalisations have not been studied in detail. Beck (1978) reported that captive dwarf crocodiles produced drumming sounds during courtship. In a review of acoustic signals produced by different crocodilian species, Dinets (2013b) listed *O. tetraspis* as producing infrasound pulses and vocal roars, but no head or jaw slaps.

In this chapter, I use continuous passive acoustic monitoring to record vocalisations of two captive adult *O. tetraspis*. I examine their acoustic activity and call parameters, presenting the first evidence of a diverse adult acoustic repertoire in a crocodylid. I further compare the calls produced in captivity to vocalisations recorded in Gabon with the acoustic monitoring system targeting forest elephants, to confirm whether these recordings were from wild *O. tetraspis*. The information on *O. tetraspis* call parameters presented here can be used for species identification and to inform monitoring and conservation projects.

4.2 Methods

I recorded two adult *O. tetraspis*, a male and a female, in Bristol Zoo Gardens UK, between 31 October and 5 December 2016. The animals were housed in an indoor enclosure containing a freshwater pool (ca. 70% of the enclosure area) and access to land (ca. 30% of the enclosure area, Fig. 4.1). Air temperature during the day ranged between 15.5–27.5°C (mean 22.3 ± 2.1°C), and during the night 15.8–24.4°C (mean 21.1 ± 2.0°C). The animals shared the enclosure with their offspring: five juvenile *O. tetraspis* which had hatched in the previous year (Schmidt, 2015), but there were no other crocodilian species house in the building. Visitors could view the enclosure from above and from the side through see-through glass panels, and during the zoo opening hours (1000–1600 hours) there was a near continuous presence of people in the building.

4.2.1 Acoustic recordings

To record the crocodiles, I used one Wildlife Acoustics SM2 acoustic recorder with an HTI-96 hydrophone and SM2 microphone set to record the sound for 58 min every hour for 32 days at 4 kHz sampling rate. To protect the hydrophone from bites, I placed it inside a 3 m long 17.5 cm diameter PVC pipe, fixed on the inside wall of the pool (Fig. 4.1). As water and PVC have similar sound transmission properties, it allowed the acoustic signal to reach the hydrophone without exposing the equipment to the animals, although its presence may have affected the underwater signals recorded. The pipe was installed a week before the recordings began, to allow the animals to habituate to the new feature in the enclosure.

The Elephant Listening Project (https://elephantlisteningproject.org/) provided further 26 minutes of acoustic recordings containing suspected wild *O. tetraspis* calls (Peter Wrege, pers. comm.). These recordings were collected over six days between April–September 2009, six days between May–August 2011, and three days between March–September 2015. Recording location

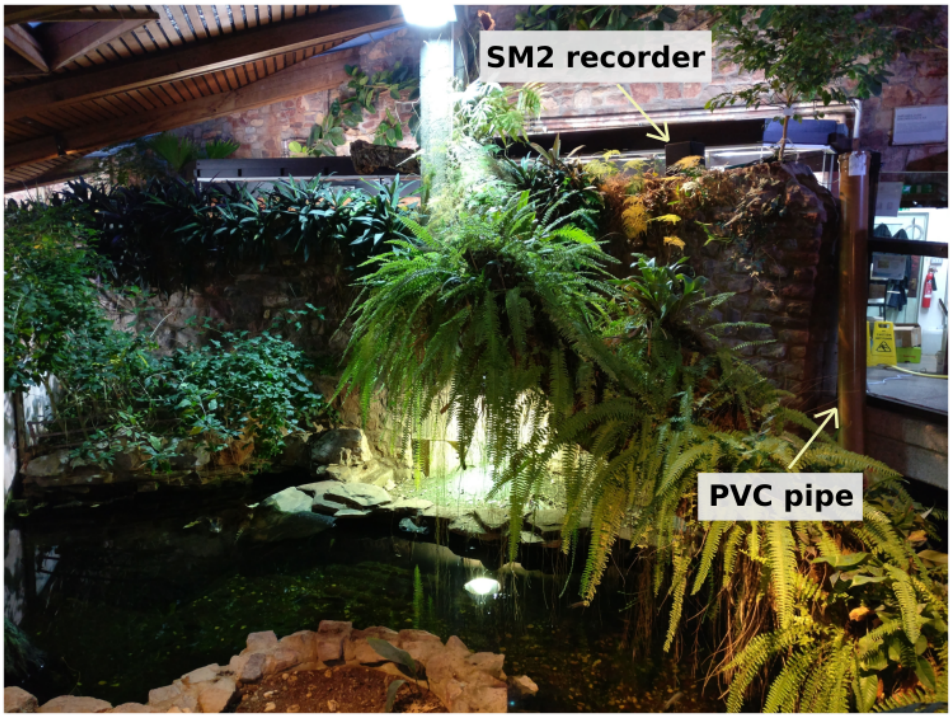

FIGURE 4.1. *Osteolaemus tetraspis* enclosure at Bristol Zoo, with marked locations of the aerial acoustic recorder (SM2+) and the PVC pipe containing the hydrophone.

was in the Ivindo National Park forest, Gabon (Fig. 2.1), using a custom-made aerial recording system recording continuously at 2kHz sampling rate (Hedwig et al., 2018). Recordings from all days except for 22 June 2009 had a time stamp, providing information on the time of recording.

4.2.2 Call analysis

I manually identified all the crocodile calls on spectrograms using SASLAB PRO 5.2.12 (Avisoft Bioacoustics, 2017) and measured the duration of each call. In the case of more complex calls composed of several pulses (where the time difference between each element was < 0.5 s) the number of pulses, the pulse duration and the inter-pulse interval were also measured. To characterise the energy distribution within the frequency spectrum of individual call types, I performed the acoustic analysis of the calls following the methods described by Chabert et al. (2015), using the SEEWAVE package for R (Sueur et al., 2008) under the following settings: FFT length = 1024; window = Hanning; overlap = 0.99. I calculated the dominant frequency (max frequency, containing most energy), the first quartile (Q25, the frequency value at 25% of the spectrum), the third quartile (Q75, the frequency value at 75% of the spectrum), the interquartile range (IQR, the difference between the first and third quartile), the centroid of the frequency spectrum (cent), the skewness (the measure of spectrum asymmetry) and the spectral flatness (SFM), i.e., the ratio between the geometric mean and the arithmetic mean of the spectrum (0 =

pure tones, 1 = noisy). To verify the measurements obtained through automatic acoustic analysis, I also manually measured the parameters in 20% of the calls using SASLAB PRO 5.2.12.

4.2.3 Statistical analysis

To characterise the acoustic properties of the call types obtained from the Bristol Zoo *O. tetraspis* and the wild crocodiles, I performed a principal component analysis (PCA) to reduce the eight acoustic parameters down to two combinations of parameters. I tested the parameter differences between the captive and wild aerial crocodile calls, and between the aerial and underwater captive crocodile calls using Mann-Whitney tests with Bonferroni correction of P values. All statistical analyses were carried out using R 3.6.0 statistical software (R Core Team, 2018).

4.3 Results

4.3.1 *Osteolaemus tetraspis* call types and call parameters

4.3.1.1 Microphone recordings: Bristol Zoo and Gabon

In total, I obtained 298 *O. tetraspis* calls, 97 recorded in Bristol Zoo and 168 from Gabon (Table 4.1). All captive calls were recorded both in the air and underwater. Wild and captive adult *O. tetraspis* produce four distinct call types, identified here as "drums", "gusts", "moos" and "rumbles" (Fig. 4.2). Drums and rumbles were characterised by low dominant frequencies (drums, $n = 161$, 31 ± 12 Hz; rumbles, $n = 75$, 40 ± 14 Hz), while gusts and moos had higher dominant frequencies (gusts, $n = 35$, 219 ± 108 Hz; moos, $n = 27$, 299 ± 133 Hz).

Rumbles also contained multiple harmonics, lasted 2.37 ± 0.77 s, and had less visible frequency modulation than the moos (Fig. 4.2). They were the second most frequent call type recorded both in captivity and in the wild, and accounted for 25% of the total *O. tetraspis* calls (Table 4.1). Rumbles were recorded on 13 days in Gabon and eight days in Bristol Zoo.

Moos were 3.90 ± 0.96 s long, had multiple harmonics with a frequency-modulating upsweep followed by a frequency-modulating downsweep (Fig. 4.2). They were the rarest type recorded, accounting for 9% of the calls. They occurred alone or in bouts of 2–5 calls on five days of recording in Bristol Zoo and five days recorded in Gabon.

TABLE 4.1. Numbers and percentage occurrence of adult *O. tetraspis* call types in recordings from Bristol Zoo and from Gabon.

Call type	Bristol Zoo	Gabon	Total
Drum	50 (51%)	111 (55%)	161 (54%)
Rumble	21 (22%)	54 (27%)	75 (25%)
Gust	17 (18%)	18 (9%)	35 (12%)
Moo	9 (9%)	18 (9%)	27 (9%)
Total	**97**	**201**	**298**

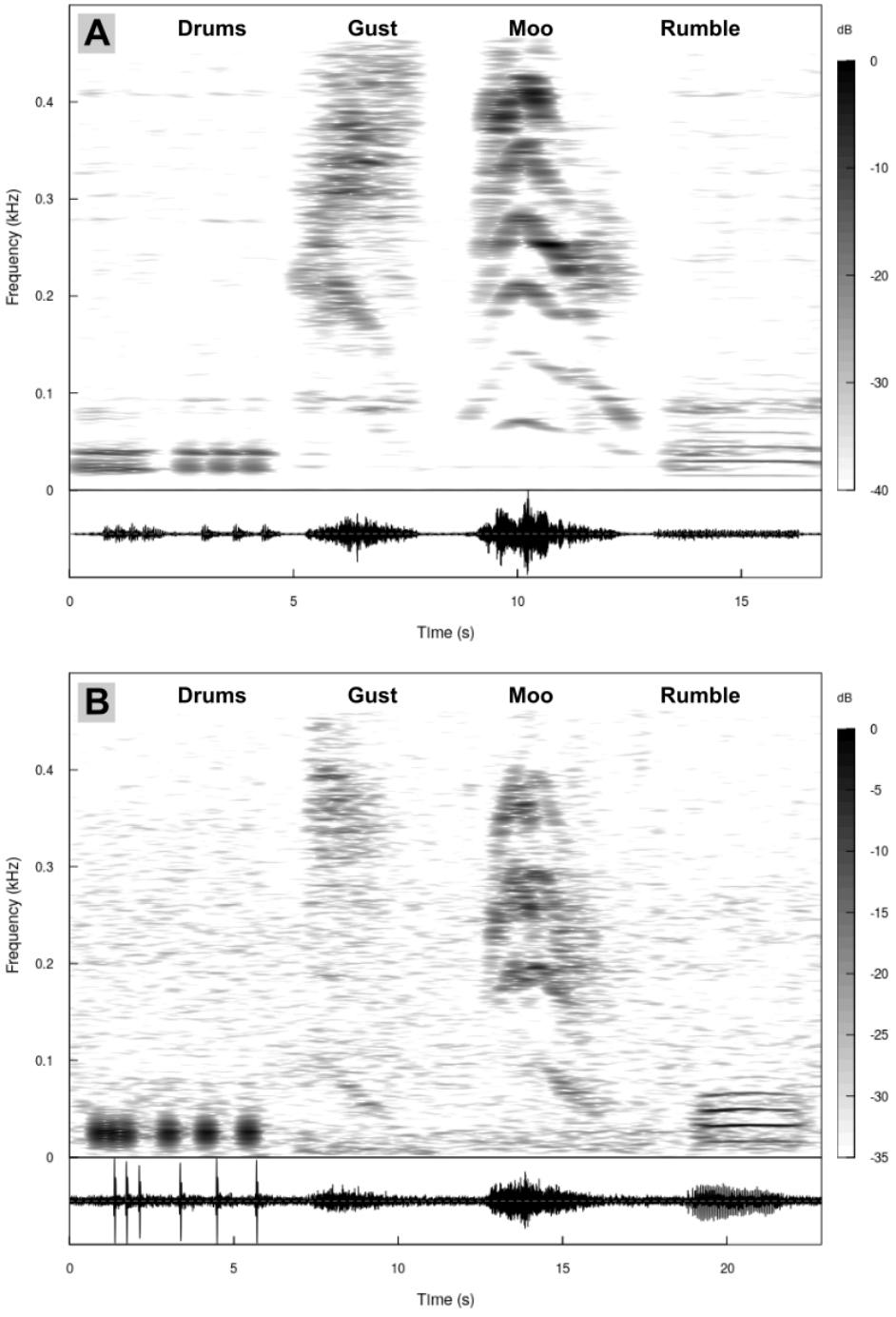

FIGURE 4.2. Composite spectrograms with examples of the four adult *O. tetraspis* call types recorded with the microphone in Bristol Zoo (A) and Gabon (B). Sampling rate 1 kHz, FFT size 1,024, Hanning window, overlap 93.75.

Gusts were 2.13 ± 0.64 s long, their energy distribution along the frequency spectrum was similar to that of moos (Table 4.4), but they did not have a visible harmonic structure. They occurred on five days of recording in Bristol Zoo, and nine days of the Gabon recordings.

Drums were the most common call type, comprising 51% of the captive calls and 55% of the wild calls recorded. They did not have a visible harmonic structure and were very short in duration, each pulse lasting 0.09 ± 0.03 s. The drums varied in composition, occurring individually or in series of 1–5 pulses. Drum series were considered a single call if the pulses were evenly spaced, with the time difference < 0.5 s between them. Single drums were most common in both captive and wild recordings, accounting for 62% of all drum calls (Table 4.2). In multiple drum calls, the time difference between the pulses lasted 0.30 ± 0.09 s. Drums were recorded on 12 different days in recordings obtained from Gabon and on 5 days of acoustic monitoring in captivity.

TABLE 4.2. Numbers and percentage occurrence of pulses in drum calls recorded in Bristol Zoo and in Gabon.

Pulses	**Bristol Zoo**	**Gabon**	**Total**
1	34 (68%)	65 (58%)	99 (62%)
2	1 (2%)	29 (26%)	30 (19%)
3	4 (8%)	12 (11%)	16 (10%)
4	9 (18%)	3 (3%)	12 (7%)
5	2 (4%)	2 (2%)	4 (2%)

The call parameters varied between the four call types. Acoustic parameters related to the energy distribution along the frequency spectrum (PC1) accounted for 61.1% of the variance between the call types, and 16.0% of variance was related to the spectral shape and duration of the call (Table 4.3). The four call types varied along the PC1 (Fig. 4.3).

TABLE 4.3. Factor loadings of the first two PCA components calculated from the nine acoustic parameters characterising the *O. tetraspis* calls. The first principal component (PC1) is related to the energy distribution along the frequency spectrum. The second principal component (PC2) is related to the spectral shape and duration of the call.

Acoustic parameter	**PC1 (61.1% expl. var.)**	**PC2 (16.0% expl. var.)**
Max. frequency (Hz)	0.397	−0.002
Q25 (Hz)	0.432	−0.021
Q75 (Hz)	0.439	−0.140
IQR (Hz)	0.415	−0.189
Cent (Hz)	0.445	−0.090
Skewness	0.140	0.679
SFM	0.055	−0.509
Duration (s)	0.266	0.465

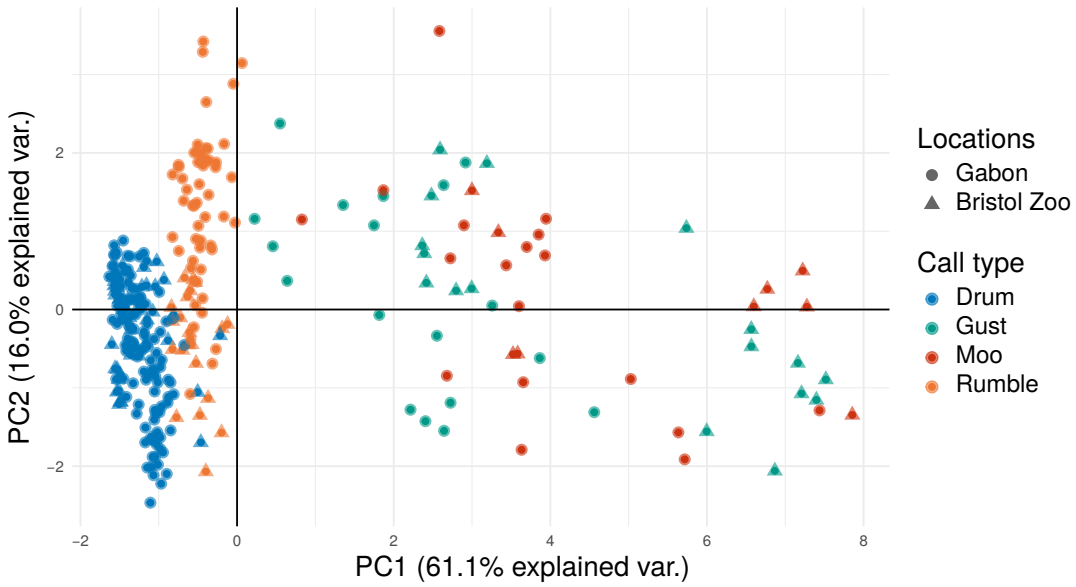

FIGURE 4.3. PCA results showing the distribution of the four adult *O. tetraspis* call types in the acoustic space. Calls were produced by produced by wild (Gabon, n unknown) and captive (Bristol Zoo, $n = 2$) individuals.

There were no significant differences in the eight acoustic parameters of the moos between the captive and wild *O. tetraspis* microphone recordings (Table 4.4). Drums differed significantly in four parameters (Q75, interquartile range, SFM and call duration), gusts in three parameters (Q25, centroid and skewness) and rumbles in five parameters (dominant frequency, Q25, Q75, centroid and skewness) between the captive and wild crocodiles (Table 4.4).

4.3.1.2 Microphone and hydrophone recordings in Bristol Zoo

The acoustic parameters of *O. tetraspis* calls were significantly different between the aerial and underwater recordings in Bristol Zoo (Table 4.5). Drums recorded underwater had a higher dominant frequency, Q25, interquartile range and centroid, as well as lower SFM. Gusts recorded underwater had a lower centroid, higher skewness and lower SFM. Moos recorded underwater had a lower centroid than the aerial recordings. Rumbles recorded underwater had a lower Q75, interquartile range, centroid and SFM than those recorded in the air.

4.3.2 Acoustic activity and call sequences

In both wild and captive recordings, most of the calls were emitted between dusk and dawn (0600–1800 hours) (Fig. 4.4). In the crocodiles at Bristol Zoo, which were recorded continuously, 93% of the calls were produced during the night, with 86% of the individual vocalisations recorded between 2000 hours (62 calls, 64%) and 2300 hours (18 calls, 19%). Out of these, 48% of the calls were drums (Fig. 4.4). In the wild recordings with a known time stamp, 81% of the calls occurred

TABLE 4.4. Acoustic characteristics (mean ± SD) of the *O. tetraspis* call types recorded with the microphone in Bristol Zoo and in Gabon: drums (n_{zoo} = 50, n_{gabon} = 111), gusts (n_{zoo} = 17, n_{gabon} = 18), moos (n_{zoo} = 9, n_{gabon} = 18) and rumbles (n_{zoo} = 21, n_{gabon} = 54). Results of Mann-Whitney (W) tests comparing the acoustic parameters between the captive and wild recordings. P-values adjusted using Bonferroni method with significance level set at 0.006. Significant P-values are presented in bold.

	Drums	**Gusts**	**Moos**	**Rumbles**
Max. freq. (Hz)				
Bristol Zoo	34 ± 16	259 ± 71	272 ± 87	51 ± 20
Gabon	30 ± 9	179 ± 122	313 ± 152	35 ± 7
W (P-value)	2,651 (0.650)	96.5 (0.065)	102 (0.291)	286.5 (< **0.001**)
Q 25 (Hz)				
Bristol Zoo	28 ± 8	223 ± 51	244 ± 59	41 ± 8
Gabon	27 ± 5	130 ± 52	185 ± 65	30 ± 3
W (P-value)	2,798.5 (0.932)	29.5 (< **0.001**)	47 (0.084)	30 (< **0.001**)
Q 75 (Hz)				
Bristol Zoo	64 ± 22	627 ± 292	693 ± 241	105 ± 22
Gabon	80 ± 30	387 ± 123	460 ± 183	85 ± 20
W (P-value)	3,589.5 (**0.003**)	82 (0.020)	33.5 (0.016)	259.5 (< **0.001**)
IRQ (Hz)				
Bristol Zoo	36 ± 16	404 ± 261	449 ± 217	63 ± 18
Gabon	53 ± 27	257 ± 111	275 ± 156	55 ± 19
W (P-value)	3,660 (< **0.001**)	125 (0.364)	46 (0.076)	371.5 (0.021)
Cent (Hz)				
Bristol Zoo	55 ± 11	464 ± 160	489 ± 141	77 ± 12
Gabon	60 ± 13	275 ± 70	344 ± 83	63 ± 9
W & P-value	3,484 (0.009)	63 (**0.002**)	34 (0.015)	193 (< **0.001**)
Skewness				
Bristol Zoo	2.13 ± 0.49	3.47 ± 1.24	3.33 ± 0.76	1.85 ± 0.51
Gabon	2.15 ± 0.51	2.40 ± 0.85	2.55 ± 0.67	3.47 ± 0.67
W & P-value	2,822 (0.865)	66 (**0.003**)	32 (0.011)	1095 (< **0.001**)
SFM				
Bristol Zoo	0.461 ± 0.110	0.557 ± 0.118	0.604 ± 0.110	0.668 ± 0.142
Gabon	0.578 ± 0.167	0.364 ± 0.262	0.549 ± 0.204	0.590 ± 0.140
W & P-value	4,001 (< **0.001**)	99 (0.077)	75 (0.781)	417 (0.078)
Duration (s)				
Bristol Zoo	0.38 ± 0.53	2.34 ± 0.60	2.97 ± 0.92	2.07 ± 0.70
Gabon	0.29 ± 0.32	1.88 ± 0.62	3.14 ± 1.00	2.49 ± 0.77
W & P-value	3,889.5 (< **0.001**)	86 (0.028)	88 (0.743)	417 (0.041)

TABLE 4.5. Acoustic characteristics (mean±SD) of the *O. tetraspis* call types recorded in the air (microphone) and underwater (hydrophone) in Bristol Zoo: drums ($n = 50$), gusts ($n = 17$), moos ($n = 9$) and rumbles ($n = 21$). Results of paired Wilcoxon (V) tests comparing the acoustic parameters between the aerial and underwater recordings. P-values adjusted using Bonferroni method with significance level set at 0.007. Significant P-values are presented in bold.

	Drums	**Gusts**	**Moos**	**Rumbles**
Max. freq. (Hz)				
Microphone	34 ± 16	259 ± 71	272 ± 87	51 ± 20
Hydrophone	51 ± 7	235 ± 44	224 ± 50	47 ± 16
V (P-value)	1,148 (< **0.001**)	48 (0.185)	7 (0.141)	51.5 (0.408)
Q 25 (Hz)				
Microphone	28 ± 8	223 ± 51	244 ± 59	41 ± 8
Hydrophone	36 ± 4	205 ± 31	204 ± 43	39 ± 5
V (P-value)	1,173.5 (< **0.001**)	45.5 (0.085)	0 (0.009)	92 (0.422)
Q 75 (Hz)				
Microphone	64 ± 22	627 ± 292	693 ± 241	105 ± 22
Hydrophone	64 ± 10	525 ± 229	508 ± 236	81 ± 15
V (P)-value	74.5 (0.036)	35 (0.027)	6 (0.055)	24 **(0.002)**
IRQ (Hz)				
Microphone	36 ± 16	404 ± 261	449 ± 217	63 ± 18
Hydrophone	28 ± 8	320 ± 221	304 ± 249	42 ± 13
V (P-value)	86.5 (< **0.001**)	45 (0.081)	11 (0.203)	20 **(0.002)**
cent (Hz)				
Microphone	55 ± 11	464 ± 160	489 ± 141	77 ± 12
Hydrophone	58 ± 7	411 ± 121	410 ± 109	63 ± 8
V (P-value)	1,012 (< **0.001**)	15 (< **0.001**)	0 **(0.003)**	19 (< **0.001**)
skewness				
microphone	2.13 ± 0.49	3.47 ± 1.24	3.33 ± 0.76	1.85 ± 0.51
hydrophone	2.41 ± 0.49	5.45 ± 1.50	4.79 ± 1.16	1.91 ± 0.50
V (P-value)	878 (0.021)	154 **(0.002)**	43 (0.012)	117 (0.973)
SFM				
microphone	0.461 ± 0.110	0.557 ± 0.118	0.604 ± 0.110	0.668 ± 0.142
hydrophone	0.393 ± 0.089	0.478 ± 0.084	0.506 ± 0.111	0.454 ± 0.103
V (P-value)	149 (< **0.001**)	16 (< **0.001**)	8 (0.098)	11 (< **0.001**)

during the night. Drums were also the most frequent nocturnal vocalisation type, accounting for 43% of the wild calls recorded.

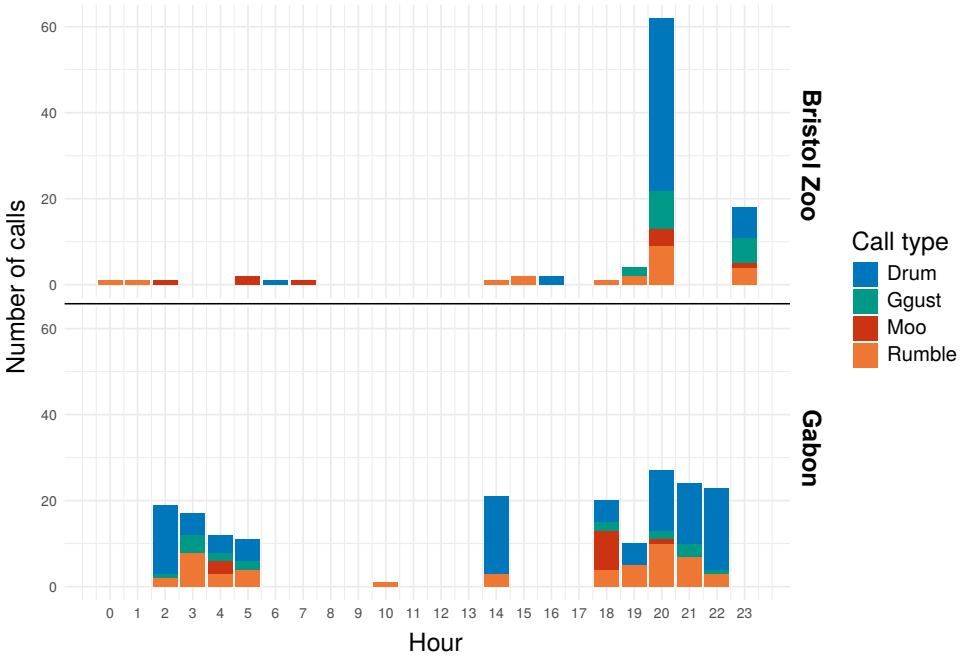

FIGURE 4.4. Frequency of *O. tetraspis* calls throughout the 24 hour period.

Sequences comprised of multiple call types arranged in the same order were recorded both in the wild and in captivity. Each sequence was formed with a rumble, followed by a gust and single or multiple drums (Fig. 4.5). The sequences occurred singly or up to five times forming bouts, and were recorded over nine days in Gabon (April–September, 23 sequences in total) and four days in Bristol Zoo (10 sequences in total). The sequences were emitted at night, between 1800–0600 hours in the wild and between 1900–2100 hours in captivity.

4.4 Discussion

The diversity of signals described here indicates that adult *O. tetraspis* have an elaborate acoustic communication system, previously described only in the Chinese alligator *A. sinensis*, (Wang et al., 2007). Similar to *O. tetraspis*, *A. sinensis* are found in ponds and small lakes with dense vegetation (Wang et al., 2007). The low dominant frequencies (< 500 Hz) attenuate less than higher frequency sounds, allowing the calls to travel further in a heavily-vegetated habitat (Wang et al., 2007). All the *O. tetraspis* calls recorded in captivity and in the wild had dominant frequencies below 400 Hz, and the diversity of acoustic signals from the very low frequency drums (31 ± 12 Hz) and rumbles (40 ± 14 Hz), to the higher frequency moos (299 ± 133 Hz) and gusts (219 ± 108 Hz), suggests that different vocalisation types may be used in long- and short-distance communication. However, low recording sampling rates, which were selected to maximise the

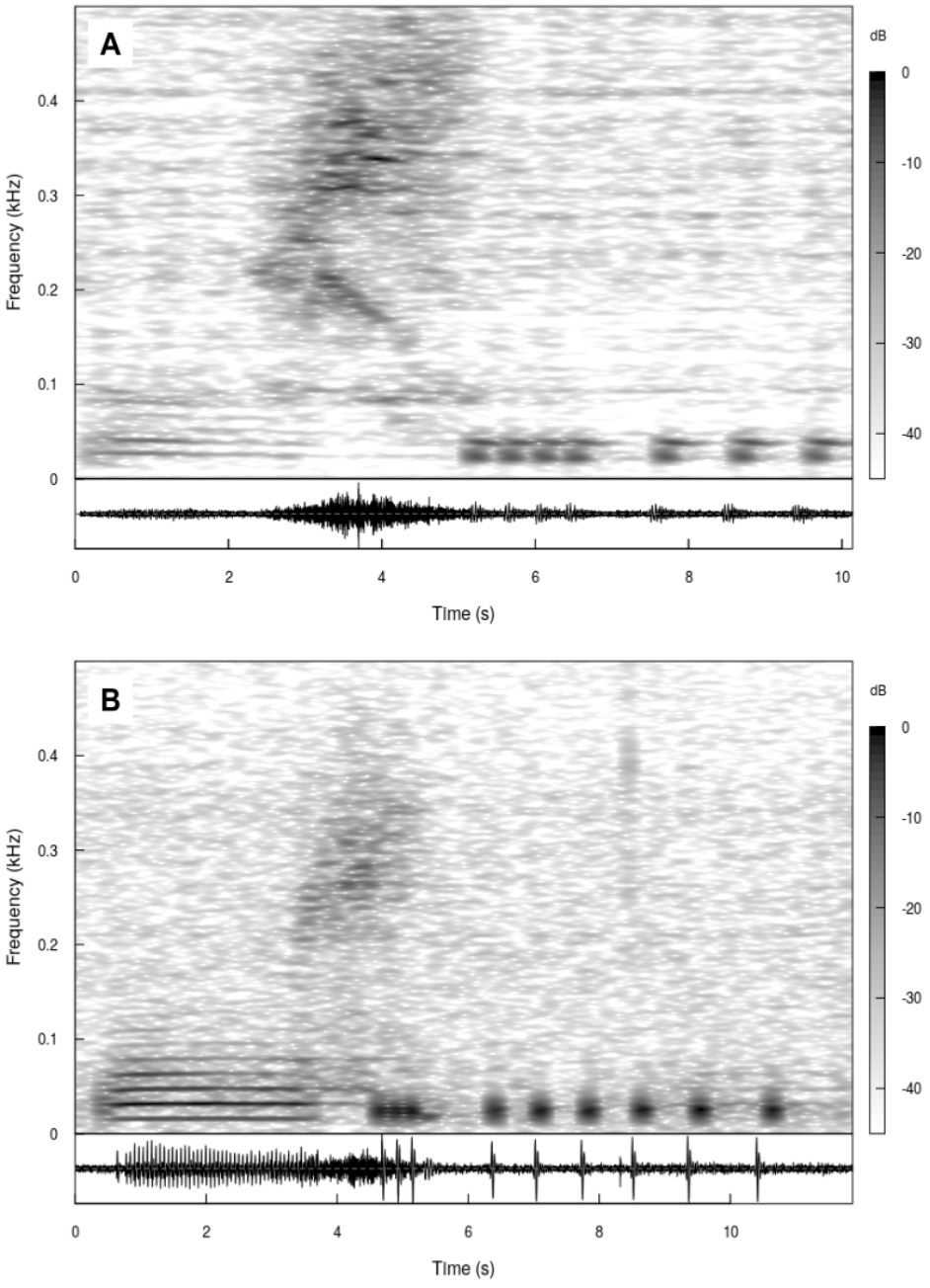

FIGURE 4.5. Call sequences of *O. tetraspis* in Bristol Zoo (A) and Gabon (B). Sampling rate 1 kHz, FFT size 1,024, Hanning window, overlap 93.75.

length of time the recorders could be left undisturbed, may have compromised the recording of higher frequency vocalisations. Thus, while *O. tetraspis* acoustic repertoire is likely similar to that of other crocodilians and composed of low-frequency sounds (Vergne et al., 2009), the lack of higher frequency recordings prevents from drawing definite conclusions.

While no typical roar was identified in the *O. tetraspis* vocalisations, both moos and rumbles could be considered a type for crocodilian roar, though differing in dominant frequency. Dinets (2013b) identified "loud" and "quiet" roars in *Crocodylus niloticus*, cough-like roars dubbed "growls" in *C. porosus*, high-pitched "groans" in *C. mindorensis* and a "groan" or "moan" produced by a captive *O. tetraspis*. Very little is known about the acoustic repertoire in many other crocodylids (Dinets, 2013b), and a higher diversity of vocal signals is possible. Although the function of the moos and rumbles in *O. tetraspis* communication is not yet known, it is likely similar to the bellows and roars produced by other crocodilians and used in courtship, dominance and territorial displays.

Drums were the most frequent call type recorded in both captive and wild animals. Their low dominant frequency suggests their similarity to the SAVs observed in other crocodilians (Todd, 2007; Grigg and Kirshner, 2015). While the SAVs are often incorporated into bellow displays in alligators, forming the first part of the bellow, they are less common in crocodylids and are not frequently reported alone (Dinets, 2013b). The function of drums is unknown. Beck (1978) observed them during *O. tetraspis* courtship in Memphis Zoo, but they were also produced in Bristol Zoo outside of the mating season and may have multiple functions depending on context. *Osteolaemus* spp. are highly terrestrial and have been found in small forest streams and isolated pools (Eaton, 2010). All calls produced in Bristol Zoo were recorded both in the air and underwater, suggesting the animals produce the sounds while on the water surface. The acoustic properties and calling pattern of drums are similar to calls emitted by cassowaries (*Casuarius* spp.). These solitary, large bodied forest-dwelling birds use infrasound communication consisting of booms, which may help them communicate in the dense tropical vegetation (Mack and Jones, 2003). The prevalence of drums in *O. tetraspis* acoustic repertoire could be an equivalent adaptation to communication in a forest habitat.

Gusts were present mainly in association with other call types, and appeared in the 33 sequences recorded in captivity and in the wild. The common sequence of rumble-gust-drums could suggest that these sequences convey a specific meaning. Combining individual vocal elements into meaningful sequences (syntax) has been demonstrated in some birds and mammals (Berwick et al., 2011; Collier et al., 2014), but this ability is yet to be confirmed in crocodilians. As crocodilians can habituate to sounds quickly (Nicolas Mathevon, pers. comm.), future playback studies on a larger number of naïve individuals are needed to test the meaning of individual call types and call sequences.

Osteolaemus are sympatric with *Mecistops* and sometimes with *Crocodylus* (Shirley and Austin, 2017). The variety of calls could also be due to sympatry (Wang et al., 2009), evolved to

avoid interbreeding, or aggressive interactions and predation with the larger crocodile species (Somaweera et al., 2013). Further research is needed to determine the effects of sympatry on crocodile acoustic signalling. However, as *Mecistops* and *Crocodylus* are generally found in larger, continuous water bodies (Waitkuwait, 1989), the forest habitat may still be the determining factor in *O. tetraspis* call repertoire evolution.

The calls from Gabon were recorded automatically while monitoring forest elephants, with the crocodile species identity initially unconfirmed (Peter Wrege, pers. comm.). Crocodilian calls vary between species and the differences are substantial enough to attribute a call to the correct species (Setner, 2008; Vergne et al., 2009). In the Ivindo National Park, *O. tetraspis* are sympatric with *M. leptorhynchus* (Shirley et al., 2018). Dinets (2013b) reported *Mecistops* roars to be similar to loud roars of many *Crocodylus* spp. and different to calls produced by *Osteolaemus* (see also Chapter 6.2.5.1). There were no significant differences between the moos produced by *O. tetraspis* in Bristol Zoo and the ones recorded in Gabon, indicating the wild calls belonged to *O. tetraspis*. The remaining call types differed significantly in 3–5 parameters (drums 4/8 different, gusts 3/8 different, rumbles 5/8 different). While the species identity of the animals recorded in the wild cannot be certain, as all three call types were part of the rumble-gust-drums sequences witnessed in captivity and recorded in the wild, the wild calls are still likely to belong to *O. tetraspis*. The significant differences in some of the call parameters (Table 4.4) could be explained by the differences between individual animals and possibly also by different recording equipment. All the calls were variable, and as crocodilian acoustic signals act as cues of their competitive ability (Reber et al., 2017), they are likely to vary between individuals. Furthermore, all the calls from Bristol Zoo belonged to just two individuals, whereas the recordings from Gabon contain an unknown number of callers, from an unknown number of populations.

Osteolaemus tetraspis are one of the more terrestrial crocodilian species, but all calls produced in Bristol Zoo were recorded both in the air and underwater, suggesting that, similar to other crocodilians (Vliet, 1989; Grigg and Kirshner, 2015), the animals produce the sounds while on the water surface. There were significant differences in captive call parameters recorded with the microphone and the hydrophone, particularly in drums (5/7 parameters different) and rumbles (4/7 parameters different). These differences could be a result of different acoustic properties of the crocodile pond and the air, and possible differences in aerial and underwater sensors.

The crocodiles were most vocal at night, with 93% of captive and 81% of wild calls recorded between 1800–0600 hours. Although the presence of zoo visitors in the daytime may have affected the behaviour of the animals, wild *O. tetraspis* are reported to be nocturnal (Waitkuwait, 1989), thus are likely to be most active after dusk. While 24 h acoustic monitoring should still be implemented in the wild to determine the call rates at different times of the day, the present data indicate that the period between 1800–0000 hours, which contained 88% of the captive and 52% of the wild calls, would be most suitable for population density monitoring and can be most easily compared with traditional spotlight eye-shine counts.

Adult crocodilians are reported to be most vocal during courtship and mating (Vliet, 1989; Vergne et al., 2009; Dinets, 2013b). Although little is known about the breeding ecology of *O. tetraspis* in the wild, nesting appears to begin in the early rainy season (Waitkuwait, 1989; Kofron and Steiner, 1994), and may be regionally asynchronous, with multiple clutches in one year (Eaton, 2010). In Gabon, the rainy season lasts from September through to May, with a short dry season in January (Lee et al., 2006). As courtship and mating predates the nest-building by about 2–3 months (Waitkuwait, 1989), the period between May–June is likely to have most courtship activity. Although the data on wild crocodile acoustic activity throughout the year were not analysed here, the presence of calls recorded between March–September in Gabon suggest a wide window of acoustic activity. Moreover, while vocalisations may be more frequent during the mating season, the captive recordings in Bristol Zoo in October–December, which were not associated with courtship or breeding activity, indicate that *O. tetraspis* may vocalise throughout the year. Further research is needed to determine the behaviour associated with the different call types and seasons.

The diversity of *O. tetraspis* acoustic signals which are detectable with aerial recorders provides basis for consideration of acoustic monitoring methods for wild *O. tetraspis* populations. Acoustic monitoring techniques are particularly suited to vocal species that are cryptic, nocturnal or difficult to access and observe, and have been successfully applied in many taxa including bats, marine mammals and elephants (Wrege et al., 2017). The crocodiles live in densely forested habitat, which can both limit observer access and conceal the animals (Riley and Huchzermeyer, 1999). As *O. tetraspis* share their habitat with other forest species of conservation concern, most notably the forest elephants *Loxodonta cyclotis*, which also share their acoustic range, further studies integrating the acoustic monitoring of different taxa could be beneficial to crocodile conservation. Despite their cryptic behaviour, and due to their small size, *Osteolaemus* are heavily hunted for bushmeat, and can comprise 22% of the non-fish bushmeat biomass sold in Central Africa (Eaton, 2009). This, combined with habitat loss and the recent taxonomic split of the genus, creates a pressing need for species assessment and monitoring (Eaton, 2010). The data presented in this chapter can provide the baseline for further research and integration of acoustic methods into *Osteolaemus* monitoring.

CHAPTER 5

RESPONSE TO DISTRESS CALLS IN WEST AFRICAN SLENDER-SNOUTED CROCODILES

Abstract

Crocodilians are very vocal, particularly as juveniles, and use acoustic communication to synchronise hatching, maintain group cohesion, and fend off threats. The distress call, produced when an individual crocodile is seized by a predator, serves to startle the predator, solicit help from conspecifics and to warn others, often kin, of the threat. While many crocodilian species stop producing distress calls as the individual grows, in the African slender-snouted crocodile *Mecistops*, the distress calls upon capture persist through adulthood. I compared distress call structure of differently sized individuals, and the responses these calls elicit from conspecifics through a playback experiment. The distress vocalisations of wild *Mecistops cataphractus* (total body length 48.6–180 cm) in Taï National Park differ between size classes, with adults producing calls with lower fundamental frequency and more energy in the lower parts of the frequency spectrum than juvenile animals. Adults and juveniles also respond significantly differently to distress calls produced by crocodiles of different body sizes. The distress calls produced by a small juvenile elicited primarily positive responses (approach, acoustic response or turning towards the source of the call) in small and large *M. cataphractus*, while adult distress calls resulted in both small and large crocodiles moving away from the source of the call. Large *M. cataphractus* also responded significantly more positively than small individuals to playbacks of distress calls made by a large juvenile. The results suggest that distress calls in *M. cataphractus* function as a way of soliciting help when emitted by a juvenile crocodile, and as a warning to conspecifics when produced by an adult. As small juvenile distress calls attract both large and small *M. cataphractus*, they could be used in species conservation management in developing a playback survey monitoring system.

5.1 Introduction

Upon encountering a predator, many aquatic and terrestrial animals, including arthropods, fish, amphibians, reptiles, birds and mammals produce distress calls (Bradbury and Vehrencamp, 2011; Knight and Ladich, 2014). These calls are loud, with a wide bandwidth and multiple harmonics, which allow for good sound propagation and localization of the source (Venuto et al., 2001; Bradbury and Vehrencamp, 2011). The calls can serve several functions. In social species, they warn nearby kin, and may attract conspecifics to mob the predator (Bradbury and Vehrencamp, 2011). For many animals, guarding the offspring is one of the primary roles of parental care, and the distress call emitted by the young can solicit parental help (Lingle et al., 2012). In solitary species where no nearby conspecifics are present, the distress call is directed at the predator in an attempt to startle it (Conover, 1994; Wise et al., 1999), attract other predators that will interfere with the attack (Bradbury and Vehrencamp, 2011), or signal good body condition of robust and difficult prey (Laiolo et al., 2004).

As modern archosaurs, crocodilians share many life history traits with birds. Both groups are oviparous, build nests, use acoustic communication at all stages of their lives, and one or both parents of almost all species will guard the nests and offspring (Cockburn, 2006; Grigg and Kirshner, 2015). In crocodilians, parental care has been observed in all genera and includes defending the nest, assisting in nest opening, carrying the young to the water, as well as defending the hatchlings (Grigg and Kirshner, 2015). Juvenile crocodilians are vulnerable to predation, with up to 95% mortality in their first year (Webb et al., 1983a; Hussain, 1999). Their predators include larger fish, toads, lizards, snakes, turtles, birds, canids, felids, humans and other crocodiles (Somaweera et al., 2013). After hatching, the juveniles will form a crèche or pod and stay together protected by a nearby adult for several weeks or months, depending on the species (Grigg and Kirshner, 2015). After that time, the adults start to show signs of aggression towards the young and crèche members disperse (Hunt and Watanabe, 1982; Grigg and Kirshner, 2015). As crocodilians grow they become less vulnerable, yet even adults can still fall prey to large constrictors and cats, other crocodiles, or humans (Somaweera et al., 2013).

Crocodilians produce a distress call when captured (Britton, 2001; Vergne et al., 2009), which appears to be analogous among the genera and has been described in *Alligator* (Hunt and Watanabe, 1982), *Crocodylus johnstoni* (Britton, 2001), *Crocodylus niloticus* (Chabert et al., 2015), *Caiman* (Vergne et al., 2012; Sicuro et al., 2013) and in the gavialids *Tomistoma schlegelii* and *Gavialis gangeticus* (Bonke et al., 2015). The distress calls are loud sounds with multiple harmonics showing a downsweeping frequency modulation of varying rate over the duration of the call (Britton, 2001). However, in some species, such as *Caiman yacare*, *C. johnstoni* and *C. niloticus*, the frequency-modulating downsweep is preceded by a frequency-modulating upsweep, giving the call a “circumflex” shape (Britton, 2001; Sicuro et al., 2013). The calls serve primarily as a way to solicit help and protection from an adult (Staton, 1978; Romero, 1983), but also provide a warning of the threat for nearby conspecifics (Britton, 2001).

While the majority of the distress calls that have been reported were produced by juvenile animals, adult crocodilians of certain species can also produce distress calls (Staton, 1978). Adult distress calls have been observed in American alligators (*Alligator mississippiensis*), common caiman (*Caiman crocodilus*), African dwarf crocodiles (*Osteolaemus* spp.) and the Western (*Mecistops cataphractus*) and Central African slender-snouted crocodiles (*Mecistops leptorhynchus*) (Staton, 1978; Shirley et al., 2018). Individual growth rates vary depending on temperature, feeding success, and position in the social hierarchy (Grigg and Kirshner, 2015), thus age cannot be easily inferred from crocodilian body size. However, crocodilian body size generally correlates with the reproductive life stage: the small hatchlings; larger, sexually-immature juveniles and sub-adults; and large, sexually-mature adults. The information about the body size of the caller is incorporated into the distress call, and Chabert et al. (2015) reported that calls of smaller-sized crocodilians elicited a stronger response from adults that came to assist the caller. Larger crocodilians encounter fewer threats, which may explain why the distress calls do not persist throughout adult life in all crocodilians (Staton, 1978; Britton, 2001).

Both species in the genus *Mecistops* are reported to be very vocal (Shirley, 2010a; Shirley et al., 2018) and animals of all body sizes have been observed producing distress calls upon capture (Matt Shirley, pers. comm.). Little is known about the social hierarchy and behaviour of *Mecistops* in the wild, including the levels of parental care, though crèches of wild *M. leptorhynchus* attended by an adult female have been observed in Gabon (Grigg and Kirshner, 2015; Shirley et al., 2018). Hypotheses linking their high rates of vocal communication with the population social structure (Shirley, 2010a) are yet to be tested. Shirley et al. (2018) noted that both *M. cataphractus* and *M. leptorhynchus* are highly responsive to distress calls, and that *M. leptorhynchus* in Gabon will often vocalise back, but rarely approach the source of the call.

In this chapter I investigate the effect of caller body size on conspecifics exposed to the distress calls in wild *M. cataphractus* from Taï National Park, Côte d'Ivoire. To determine whether distress calls differ with body size, I compare the acoustic parameters of calls produced by small and large juveniles and by adult *M. cataphractus*. I test whether distress calls produced by small juveniles, large juveniles and adults elicited different responses from their conspecifics. As distress calls function primarily as a way for young animals to solicit protection from their parents, I predict approach responses from adults upon hearing small juvenile calls, and for these responses to diminish with increasing size of the caller. To determine whether distress calls, particularly those emitted by larger juveniles and adults that do not rely on parental protection, also function as a warning, I test for differences in the types of responses produced by adult and juvenile *M. cataphractus* to the distress calls of each size class. If the distress calls function as a warning to conspecifics, I predict other crocodiles to move away from the source of the distress call. I further provide the first description of the acoustic parameters of the wild juvenile and adult *M. cataphractus* distress calls.

5.2 Methods

5.2.1 Capture and acoustic recordings

I captured six *M. cataphractus* (48.6–180 cm total length) on the Hana River, south-western Taï National Park, Côte d'Ivoire between 11–24 April 2018 (for study site description see Chapter 2.1.2). The crocodiles were located at night from a motorised boat using a spotlight. Smaller individuals were caught using tongs, and larger animals we caught using a snare pole. All animals began vocalising immediately upon capture and were recorded using a hand-held Roland R-05 recorder with built-in stereo microphones (sampling rate 44.1 kHz, frequency range 20–40,000 Hz), held approx. 50 cm from the animal's head. Each distress vocalisation bout lasted approx. 2 min, after which the animal was released back into the water.

5.2.2 Call analysis

I recorded calls from six *M. cataphractus*, including small juvenile ($n = 1$, 48.6 cm total length), large juvenile ($n = 4$, 81.0 ± 10.7 cm total length) and adult ($n = 1$, 180.0 cm total length) individuals. From each vocalisation bout, 1–20 calls were selected for analysis: small juvenile ($n = 20$), large juveniles ($n = 39$) and adult ($n = 20$). I measured the duration of each call using SASLAB PRO 5.2.12 (Avisoft Bioacoustics, 2017) and performed the acoustic analysis of the calls following the methods described by Chabert et al. (2015), using the SEEWAVE R package (Sueur et al., 2008) and PRAAT 6.0.43 software (Boersma and Weenink, 2018).

To describe the energy distribution within the frequency spectrum of individual distress calls, I used SEEWAVE (FFT length = 1024, window = Hanning, overlap = 99%, bandwidth 0–5kHz) to calculate the dominant frequency (max. frequency), the first and third quartiles (Q25 and Q75, frequency value at 25% and 75% energy spectrum), the interquartile range (IQR, the difference between the first and third quartile), the centroid of the frequency (cent), the skewness (the measure of spectrum asymmetry), the kurtosis (the measure of spectrum peakedness) and the spectral flatness (SFM), i.e., the ratio between the geometric mean and the arithmetic mean of the spectrum (0 = pure tones, 1 = noisy).

To characterise the fundamental frequency of the calls (the pitch), I extracted the pitch contour using PRAAT following Chabert et al. (2015). I analysed a narrow band (0–2,000 Hz) of the signal spectrogram and manually corrected any errors of the automatically measured pitch contour. I measured the fundamental frequency value at the beginning of the call (start pitch), the minimum and maximum values (min. and max. pitch), the mean fundamental frequency (mean pitch) and the fundamental frequency value at the end of the call (end pitch).

5.2.3 Playback experiment

Using SASLAB PRO, I prepared the playback sequences for the three caller size classes. For each size class, a single individual was used: small juvenile (48.6 cm total body length), large juvenile

with the clearest call sequence and intermediate size (78 cm total body length), and adult (180 cm total body length). Each recording was normalised to 95% volume and trimmed to obtain a natural call sequence of 51 ± 12 seconds and 27 ± 5 individual vocalisations. Two sequences (I and II, see Table 5.1) were created for each size class.

I performed the playback experiments on six nights (1900–0300 hours), between 25 April and 12 May, 2018. During each night, I played the three distress call sequences (small juvenile, large juvenile and adult *M. cataphractus*) from the boat at 400 m intervals along three 8.2 ± 1.4 km stretches of the Hana River, using an Ultimate Ears Wonderboom portable Bluetooth speaker (frequency range 80–20,000 Hz) set at maximum volume. Each river section was surveyed twice, thus to minimise the risk of repeated exposure of the animals to the same signal, I played a different playback sequence (I or II) from each size class (Table 5.1) when repeating the experiment over a previously surveyed river section. There were 14 ± 2 playback points per survey (86 intervals in total). At every playback point, one call sequence from each size class was played in a randomised order, with 30 s break between call sequences. Two observers were monitoring the river with spotlights and noting down the presence, behaviour and estimated body size of any crocodiles before, during and after each of the playback sequences was played.

TABLE 5.1. Sequence duration (s) and number of individual calls in the playback distress call sequences of *M. cataphractus* of each size class.

Caller size class	**Body length (cm)**	**Sequence I**	**Sequence II**
Small juvenile	48.6	29 calls, 58 s	22 calls, 61 s
Large juvenile	78.0	22 calls, 60 s	26 calls, 37 s
Adult	180.0	35 calls, 39 s	30 calls, 36 s

Behavioural response types were catalogued (Table 5.2) and ranked according to the strength of the response, from negative (−1) to extremely positive (4). In order to test for differences between the responses of small (< 140 cm body length) and large (> 140 cm body length) crocodiles to calls of different size classes, I grouped the *M. cataphractus* responses to playback into three categories: negative (−1), neutral (0) and positive (1–4). At 46 playback location points there were no crocodiles sighted throughout the entire playback trial. These points were removed from the analysis.

5.2.4 Statistical analysis

To characterise the acoustic properties of the calls of individuals from different size classes, I performed a principal component analysis (PCA) to reduce the number of acoustic parameters from 14 to two. I tested the parameter differences between the three size classes using Kruskal-Wallis and Dunn tests for multiple comparisons. I adjusted the P-values using Benjamini-Hochberg correction. I compared the total counts of each reaction types between the groups using a chi-square test. All statistical analyses were performed using R 3.6.0 (R Core Team, 2018).

TABLE 5.2. Ethogram of behavioural responses to *M. cataphractus* distress call playback, categorised into negative, neutral and positive types.

Category	Name	Description
Negative (−1)	Retreat	Moving away from the source of the call or submerging.
Neutral (0)	No response	No visible response.
Positive (1)	Turn	Turning the head towards the source of the call or swimming in parallel to the speaker (neither retreating nor approaching).
Positive (2)	Vocalise	Producing a vocal response.
Positive (3)	Tail ride	Splashing water while propelling the body with the tail and raising the body above the water (Shirley et al., 2018).
Positive (4)	Approach	Swimming towards the source of the call.

5.3 Results

5.3.1 Call parameters

All *M. cataphractus* distress calls had multiple harmonics, with a frequency-modulating upsweep followed by a frequency-modulating downsweep (Fig. 5.1). The call parameters varied with body size. Acoustic parameters related to fundamental frequency and energy distribution (PC1) accounted for 57.8% of the variance between the three size classes, while 23.9% of variance was related to the spectral shape and duration (PC2) of the call (Table 5.3). The calls of *M. cataphractus* of different size classes varied along the PC1 spectrum (Fig. 5.2).

TABLE 5.3. Factor loadings of the first two PCA components calculated from the 14 acoustic parameters characterising the *M. cataphractus* distress calls. The first principal component (PC1) is related to fundamental frequency and energy distribution along the frequency spectrum. The second principal component (PC2) is related the spectral shape and the duration of the call.

Acoustic parameter	PC1 (57.8% expl. var.)	PC2 (23.9% expl. var.)
Mean pitch (Hz)	0.312	−0.251
Start pitch (Hz)	0.320	−0.183
Max. pitch (Hz)	0.299	−0.201
Min. pitch (Hz)	0.285	−0.283
End pitch (Hz)	0.283	−0.285
Max. freq. (Hz)	0.315	0.069
Q25 (Hz)	0.319	0.016
Q75 (Hz)	0.326	0.172
IQR (Hz)	0.170	0.258
Cent (Hz)	0.347	0.073
Skewness	−0.128	−0.502
Kurtosis	−0.116	−0.479
SFM	0.254	0.338
Duration (s)	0.164	−0.329

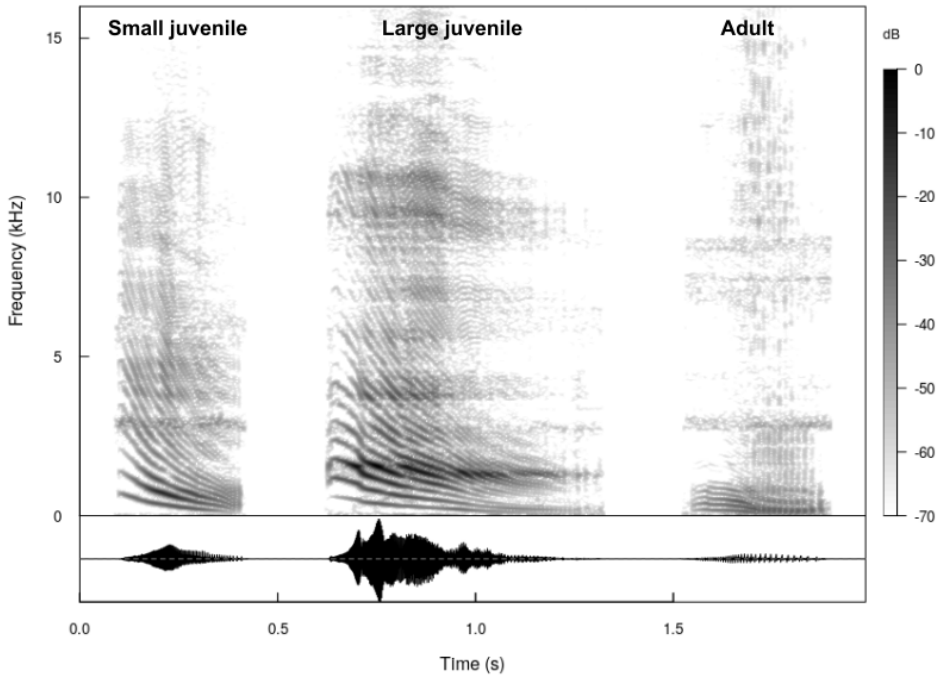

FIGURE 5.1. A composite spectrogram of normalised small juvenile (48.6 cm), large juvenile (78 cm) and adult (180 cm) *M. cataphractus* distress calls. FFT size 1,024, Hanning window, overlap 93.75.

All acoustic parameters, except for the skewness and kurtosis, were significantly different between the size classes (Table 5.4). The adults produced calls with a significantly lower fundamental frequency and more energy in the lower parts of the frequency spectrum than small and large juveniles (Tables 5.4, 5.5). Adult calls also had a significantly lower spectral flatness (SFM) than small and large juvenile calls (Table 5.5).

Small juvenile distress calls also had significantly lower mean, start and maximum fundamental frequency than those of large juveniles, but there were no significant differences in the minimum or end pitch between the two size classes (Table 5.5). The calls of the small juvenile also had more energy in the lower parts of the frequency spectrum than calls of large juveniles (Tables 5.4, 5.5). Large juveniles produced longer calls than the small juvenile and adult (Table 5.5). However, there was no significant difference in call duration between the small juvenile and adult crocodiles (Table 5.5).

5.3.2 Acoustic parameter variation within the large juvenile distress calls

The acoustic parameters of the *M. cataphractus* distress calls also varied within the large juvenile size class (Fig. 5.2). The 78 cm long juvenile used in the playback experiment produced significantly longer calls, lasting 0.61 ± 0.54 seconds, compared to the calls of the non-playback

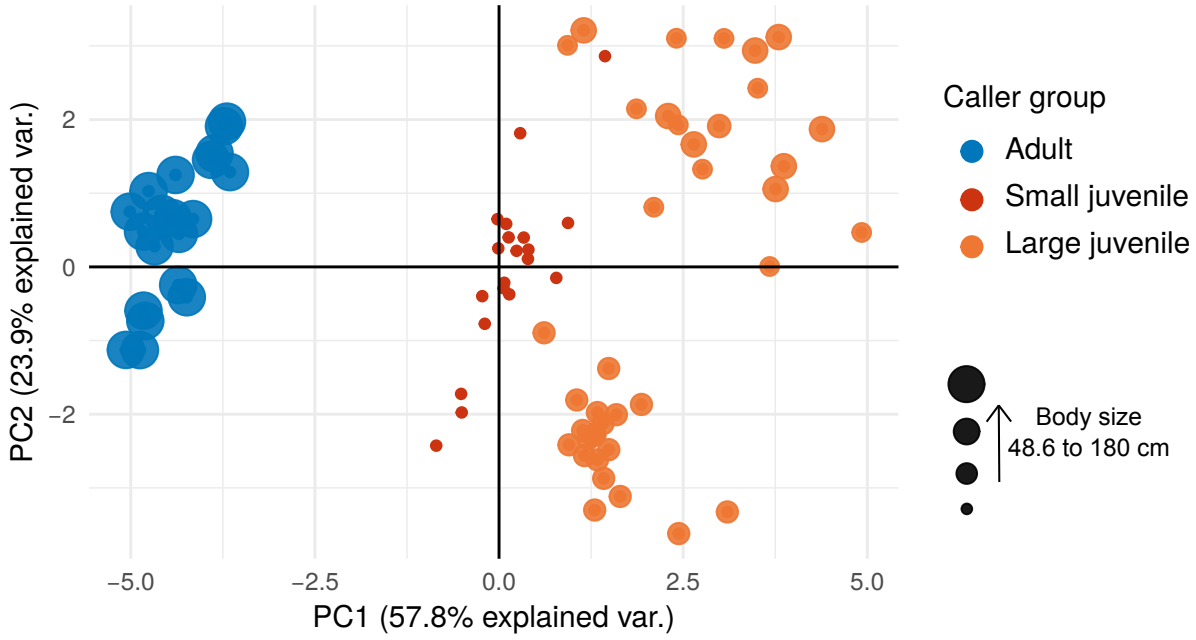

FIGURE 5.2. PCA results showing the distribution of distress calls of different *M. cataphractus* size classes in the acoustic space. The small juvenile ($n = 1$, 48.6 cm body length) is shown in red, large juveniles ($n = 4$, 81.0 ± 10.7 cm body length) in orange, and adult ($n = 1$, 180.0 cm body length) in blue.

TABLE 5.4. Acoustic characteristics (mean ± SD) of the distress calls of small (juv. S) juvenile ($n = 1$, 48.6 cm body length, 20 calls), large (juv. L) juvenile ($n = 4$, 81 ± 10.7 cm body length, 39 calls) and adult ($n = 1$, 180.0 cm body length, 20 calls) *M. cataphractus*. Results of Kuskal-Wallis groups comparison tests: χ^2 with df = 2. Significant *P*-values are presented in bold.

Acoustic parameters	**Juv. (S)**	**Juv. (L)**	**Adult**	**χ^2 (*P*)**
Mean pitch (Hz)	305 ± 13	354 ± 67	116 ± 14	52.661 (< **0.001**)
Start pitch (Hz)	458 ± 32	548 ± 100	174 ± 21	55.033 (< **0.001**)
Max. pitch (Hz)	445 ± 68	559 ± 119	175 ± 22	55.43 (< **0.001**)
Min. pitch (Hz)	187 ± 16	194 ± 47	60 ± 16	46.206 (< **0.001**)
End pitch (Hz)	187 ± 16	195 ± 49	60 ± 16	46.206 (< **0.001**)
Max. freq. (Hz)	700 ± 44	1,953 ± 473	202 ± 44	66.492 (< **0.001**)
Q 25 (Hz)	598 ± 37	1,478 ± 292	191 ± 26	66.992 (< **0.001**)
Q 75 (Hz)	2,257 ± 393	2,464 ± 656	783 ± 241	44.545 (< **0.001**)
IRQ (Hz)	1,659 ± 379	986 ± 456	592 ± 219	35.851 (< **0.001**)
Cent (Hz)	1,488 ± 147	2,067 ± 366	554 ± 107	62.35 (< **0.001**)
Skewness	2.24 ± 0.55	1.84 ± 0.75	2.10 ± 0.38	3.6847 (0.158)
Kurtosis	7.92 ± 2.45	6.39 ± 2.56	7.26 ± 1.92	4.5893 (0.100)
SFM	0.634 ± 0.670	0.650 ± 0.140	0.473 ± 0.101	19.003 (< **0.001**)
Duration (s)	0.316 ± 0.16	0.499 ± 0.137	0.282 ± 0.047	46.831 (< **0.001**)

TABLE 5.5. Results of Dunn tests for multiple pairwise comparisons between significantly different acoustic parameters from Table 5.4 for small juvenile (juv. S), large juvenile (juv. L), and adult. *P*-values are adjusted using Benjamini-Hochberg.

Acoustic parameters	**Juv. (S) / juv. (L)**	**Juv. (S) / adult**	**Juv. (L) / adult**
Mean pitch (Hz)	**0.004**	< **0.001**	< **0.001**
Start pitch (Hz)	< **0.001**	< **0.001**	< **0.001**
Max. pitch (Hz)	< **0.001**	< **0.001**	< **0.001**
Min. pitch (Hz)	0.133	< **0.001**	< **0.001**
End pitch (Hz)	0.133	< **0.001**	< **0.001**
Max. frequency (Hz)	< **0.001**	**0.006**	< **0.001**
Q 25 (Hz)	< **0.001**	**0.006**	< **0.001**
Q 75 (Hz)	0.644	< **0.001**	< **0.001**
IRQ (Hz)	< **0.001**	< **0.001**	**0.007**
Cent (Hz)	< **0.001**	**0.003**	< **0.001**
SFM	0.688	< **0.001**	< **0.001**
Duration (s)	< **0.001**	0.135	< **0.001**

large juveniles with calls 0.38 ± 0.08 seconds long (Table 5.6). The calls of the juvenile used in the playback experiment had more energy in the lower parts of the frequency spectrum than those of the non-playback juveniles, as well as significantly higher mean, minimum and end fundamental frequency, the spectral skewness and kurtosis (Table 5.6). The calls of the non-playback juveniles had a significantly higher spectral flatness, indicating noisier sounds, than those of the juvenile used in the playback experiment (Table 5.6).

TABLE 5.6. Acoustic characteristics (mean ± SD) of the calls of the large juvenile used in the playback experiment (78 cm body length) and the three large juveniles not used in the playback experiment (80 ± 13 cm body length). Results of Mann-Whitney (*W*) tests comparing acoustic parameters between the groups ($n_{playback}$ = 20, $n_{non-playback}$ = 19). Significant *P*-values are presented in bold.

Acoustic parameters	**Playback**	**Non-playback**	***W* (*P*)**
Mean pitch (Hz)	377 ± 60	329 ± 67	115 **(0.035)**
Start pitch (Hz)	556 ± 84	539 ± 116	204 (0.708)
Max. pitch (Hz)	583 ± 97	535 ± 138	180 (0.792)
Min. pitch (Hz)	214 ± 28	173 ± 54	109 **(0.022)**
End pitch (Hz)	216 ± 32	173 ± 54	104 **(0.015)**
Max. frequency (Hz)	$1,591 \pm 84$	$2,334 \pm 407$	343 (< **0.001**)
Q 25 (Hz)	$1,291 \pm 29$	$1,675 \pm 316$	329 (< **0.001**)
Q 75 (Hz)	$1,863 \pm 126$	$3,096 \pm 264$	380 (< **0.001**)
IRQ (Hz)	572 ± 122	$1,421 \pm 199$	380 (< **0.001**)
Cent (Hz)	$1,749 \pm 58$	$2,401 \pm 224$	380 (< **0.001**)
Skewness	2.48 ± 0.19	1.17 ± 0.45	0 (< **0.001**)
Kurtosis	8.51 ± 1.20	4.17 ± 1.44	5 (< **0.001**)
SFM	0.518 ± 0.022	0.788 ± 0.037	380 (< **0.001**)
Duration (s)	0.614 ± 0.544	0.377 ± 0.078	9 (< **0.001**)

5.3.3 Behavioural responses to *Mecistops cataphractus* alarm calls

Crocodiles were observed at 40 of the 89 playback points, and responses to the total 120 individual playback sequences were analysed. There was no significant difference in the identity of the first playback caller at the 40 points where crocodiles were observed (small juvenile $n = 17$; large juvenile $n = 11$; adult $n = 12$; $\chi^2 = 1.554$, df = 2, $P = 0.460$). In total, 52 responses from 22 large (adult) animals, and 96 responses from 34 smaller (juvenile) crocodiles were recorded (Table 5.7). Responses to playback sequences were observed immediately, usually within 1–5 s of a sequence being played.

TABLE 5.7. Numbers of large (adult) and smaller (juvenile) *M. cataphractus* responses to smaller juvenile, larger juvenile and adult *M. cataphractus* distress calls.

Caller size class	**Small juvenile**	**Large juvenile**	**Adult**
Responses by small crocodiles (< 140 cm)	34	34	28
Responses by large crocodiles (> 140 cm)	18	15	19
Total responses	52	49	47
Total playback trials	40	40	40

The responses to alarm calls of 48.6 cm, 78 cm and 180 cm long *M. cataphractus* differed significantly within both large ($\chi^2 = 22.779$, df = 4, $P < 0.001$) and small ($\chi^2 = 28.864$, df = 4, $P < 0.001$) crocodiles. In both groups, the alarm calls of a small juvenile elicited mainly positive responses, with 94.4% of large and 67.6% of small *M. cataphractus* reacting in a way that signals attentiveness to the small juvenile call ($\chi^2 = 4.795$, df = 2, $P = 0.091$; Fig. 5.3). The alarm calls of the adult *M. cataphractus* resulted in both large (63.2%) and small (46.4%) crocodiles moving away ($\chi^2 = 2.281$, df = 2, $P = 0.320$; Fig. 5.3). Large *M. cataphractus* responded significantly more positively than the small individuals to large juvenile distress calls ($\chi^2 = 10.548$, df = 2, $P = 0.005$), with 66.7% of large vs 17.9% of small crocodiles responding (Fig. 5.3). There were no significant differences between large and small crocodiles in response to small juvenile ($\chi^2 = 4.795$, df = 2, $P = 0.091$) and adult ($\chi^2 = 2.281$, df = 2, $P = 0.320$) distress calls.

5.4 Discussion

The acoustic analysis shows that the distress vocalisations of West African slender-snouted crocodiles differ between the size classes, with the adult calls having a lower fundamental frequency and more energy in the lower parts of the frequency spectrum than those of juveniles. Adult distress calls elicited mostly negative reactions from both juvenile and adult *M. cataphractus*, which moved away from the source of the call. In contrast, both adults and juveniles reacted positively to distress calls of a small juvenile *M. cataphractus*, either by approaching, giving an acoustic response or turning their body towards the source of the call. Adults also reacted more positively than juveniles to the distress calls of a large juvenile.

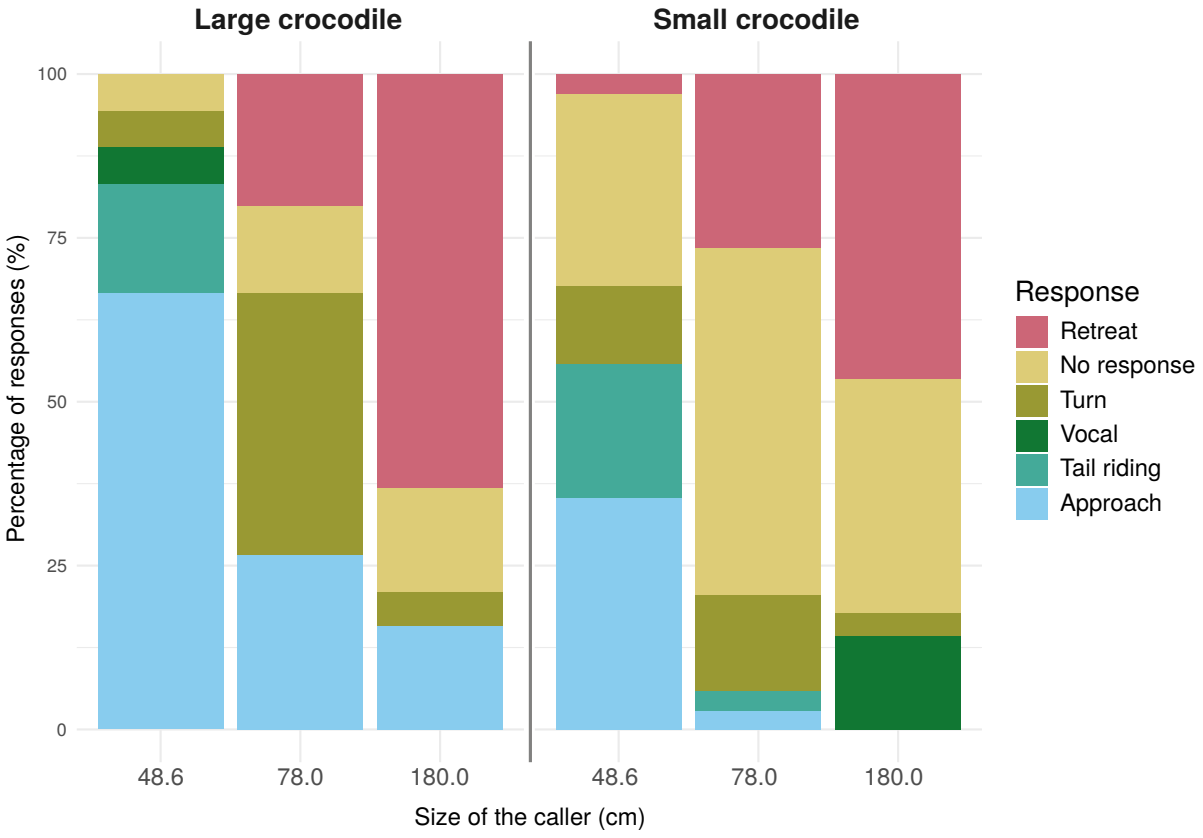

FIGURE 5.3. Percentages of negative (retreat), neutral (no response) and positive (turn, vocal, tail riding/splashing or approach) responses to distress calls of small juvenile (48.6 cm body length), large juvenile (78 cm) and adult (180 cm) *M. cataphractus* by wild large (> 140 cm) and small (< 140 cm) crocodiles. Negative responses are shown in red, neutral in yellow, and positive in the green-blue gradient.

The distress call structure of *M. cataphractus* follows a "circumflex" pattern similar to that found in *C. johnstoni*, *C. niloticus* and *C. yacare* (Britton, 2001; Vergne et al., 2009; Sicuro et al., 2013). While the pitch and energy distribution of *M. cataphractus* distress calls decreased with body size from juveniles to adult, these parameters were higher in the calls of the larger juveniles than the small one. This unusual result could be the effect of individual variation and the small sample size. Similar increase in call frequency in the neighbouring juvenile size class was seen in other crocodilian species tested by Chabert et al. (2015) where the small number of smaller animals were recorded. In both *A. mississippiensis* and *Crocodylus intermedius*, multiple juveniles ranging 60–80 cm long produced distress calls with higher pitch and maximal energy than the single 40–60 cm long representatives of their species (Chabert et al., 2015). In contrast, multiple individuals from each size class of *C. niloticus* showed a consistent decrease in pitch and energy distribution with the body size increase (Chabert et al., 2015).

Individual variation was also present within the size class of the four larger juveniles. The 78 cm long individual used in the playback produced distress calls that were on average 0.237 seconds longer, with more energy in the lower parts of the frequency spectrum than those of other crocodiles in its size class. The distress calls can vary between the same-sized individuals (Sicuro et al., 2013) as well as within the individual's call range. Crocodilians are able to adjust the intensity and pitch of their calls by changing the mouth aperture (Vergne et al., 2009), and Herzog and Burghardt (1977) differentiated between a low pitch "moan" and a louder, higher pitch "screech" call. While those variations could be due to variations in the body size of tested animals, Gorzula (1985) suggested differences in response to handling by different crocodiles. Thus, the differences in calls, such as the longer, lower-pitched, less noisy calls of the 78 cm long individual could be related to the stress level, the perceived threat, and also the time spent being handled. As most wild crocodilians vocalise loudly when handled by humans (Grigg and Kirshner, 2015), it is likely that the capture produces a similar distress call in wild *M. cataphractus* as that of being seized by a predator. However, the extent of predation context given by human capture and its effects on the crocodile distress call are not always clear and Gorzula (1985) observed varying levels of responses from *Caiman crocodilus* exposed to calls of different hatchlings being handled.

The *M. cataphractus* responses to distress calls varied with the size of the caller and the size of the responding crocodile. The small juvenile call attracted positive responses from both juvenile and adult *M. cataphractus*. The crocodiles either turned to face the caller, gave an acoustic response (either vocal or through splashing water and tail riding), or approached the speaker. As the main function of the distress call is thought to be solicitation of help from an adult during an attack (Staton, 1978; Britton, 2001), the high rate of positive adult responses, 66.6% of which involved approaching the source of the call, could be explained as parental protection. Crocodilians do not discriminate between their offspring distress calls and those of unrelated individuals (Romero, 1983; Vergne et al., 2009). Adult *C. yacare* attending a crèche will rapidly approach the source of the distress call performed by hatchlings from a different nest as well as their own (Sicuro et al., 2013).

In *Caiman crocodilus*, hatchling distress calls have been shown to attract adults but repel other hatchlings, suggesting that another function of the distress call in this species is a warning signal for vulnerable conspecifics (Staton, 1978; Romero, 1983). In contrast, although hatchling *M. cataphractus* were not available at the time of the study, the responses of juvenile crocodiles to distress calls of a small juvenile were primarily positive and not significantly different to adult responses. Juvenile *M. cataphractus* also produced more acoustic responses, including splashing water while propelling themselves with the tail and raising their body above the water, described by Shirley et al. (2018) as "tail riding". While there are anecdotal reports of *M. cataphractus* tail riding in Ghana and Côte d'Ivoire, the behaviour has not been documented in other crocodilian species, particularly in the context of distress calls. As it was primarily performed by larger

juveniles in response to a smaller juvenile call, it may be an example of an assistance response, with the aim of intimidating the attacker with the noise and sudden movement.

Adult *M. cataphractus* responded significantly more positively than juveniles to large juvenile calls. However, fewer of the responses (26.6%) involved approaching the source of the call. In most crocodilians parental protection lasts between a few weeks to a few months, after which the offspring disperse to fend for themselves (Grigg and Kirshner, 2015). The distress call contains information about the body size of the caller, and adult *C. niloticus* are less receptive to calls of larger juveniles (Chabert et al., 2015). As crocodilians grow, they become less vulnerable to predation and the body size of potential predators increases, posing a bigger threat to the crocodile providing help. This may also explain why few of the juvenile *M. cataphractus* responded positively to the large juvenile distress call.

Both juveniles and adults produced response calls to the distress playbacks, though these reactions were less frequent than a response that involved approaching the source of the call. Vocalisations in response to distress calls have also been reported in hatchling *C. crocodilus* (Romero, 1983), but crocodilians of all size classes have been observed to produce response calls (Britton, 2001). Vocalisation responses were commonly observed in *M. leptorhynchus* in Gabon (Matt Shirley, pers. comm.), and Shirley et al. (2018) noted that this type of response to distress calls was more common than approach for that species. The role of these vocalisations is unknown, and it is possible that it may have different functions depending on the context (Gorzula, 1985). While behavioural differences between the allopatric *M. cataphractus* and *M. leptorhynchus* could be the reason for the observed differences in the rate of vocalisation and approach in response to distress calls, context variations resulting from different environments in Gabon and Côte d'Ivoire, capture methods, as well as survey and playback equipment, could also contribute to the response rate differences between the species.

Adult distress calls are not commonly observed in many of the crocodilian species, with the exception of some alligatorids (Staton, 1978) and *Mecistops* (Shirley et al., 2018). As larger crocodiles have few natural predators, the ones that are capable of seizing a large crocodile will likely not be deterred by assistance of other crocodiles. Thus, the adult distress call is less likely to function as a way of soliciting help, and more as a warning signal to others. In this study, the adult *M. cataphractus* distress calls led to the retreat of 46.4% of small and 63.2% of large crocodiles exposed to the calls. While distress calling could be seen as an example of altruistic behaviour, Staton (1978) suggested that distress calls evolved as the benefit to the caller in early life stages when they elicit the parental protection, and their benefit to conspecifics as a warning signal is incidental. Furthermore, retaining the distress call in adult life, that is observed in some species, is caused primarily by the lack of negative selection for producing this signal in later life.

Both *A. mississippiensis* and *C. crocodilus*, which have been observed producing distress calls as adults, display a wide range of social behaviours and can be found living in large groups, with many animals likely living in proximity to their kin (Garrick and Lang, 1977; Staton, 1978; Grigg

and Kirshner, 2015). *Mecistops cataphractus* is listed as Critically Endangered in the IUCN Red List of Threatened Species (Shirley, 2014), and with their populations decreasing, large groups of individuals are not encountered. Although little is known about their social structure in the wild, retaining the distress vocalisations through adulthood, which serve as a warning signal to nearby conspecifics, could indicate that they displayed a social structure more similar to the gregarious, rather than solitary crocodilian species.

One of the main drawbacks of working with a rare species is the low number of animals available, particularly in the small juvenile and adult size classes, which contained a single individual each. With only one small juvenile *M. cataphractus* captured and no hatchlings encountered during the study, little is known about the effect of small juvenile distress calls on crocodiles in the same size class. Adult *M. cataphractus* can reach 2.5–3 m in length and the species is thought to reach sexual maturity at 1.9–2 m (Shirley et al., 2018). The 1.8 m *M. cataphractus* was the largest crocodile captured during the study, and while it was close to being sexually mature and thus was considered an adult, a comparison with a greater number of larger individuals could provide more information on the function of adult distress calls. Additionally, as the 1.8 m *M. cataphractus* rolled during the capture, its snout was shut with the snare rope, which resulted in more muffled calls being recorded, than those that can be obtained from individuals with their palatal valve open (Britton, 2001). The closed palatal valve lowers the call frequency and amplitude (Britton, 2001), though normalising the amplitude of all playback calls to 95% aimed to remove the effect of closed mouth on recorded amplitude. Further studies using calls obtained from a larger number of crocodiles would provide more information on individual variation within the size classes.

Furthermore, responses of adult *C. niloticus* to playback have been reported to be slow and delayed (Vergne et al., 2012; Chabert et al., 2015), possibly due to hunting pressure resulting in wariness in adult animals (Nicolas Mathevon, pers. comm.). While *M. cataphractus* in Taï National Park were observed responding immediately upon hearing the playback sequences, suggesting that the 30 s intervals between sequences were sufficient, possible delays in some observed responses could not be excluded. Thus, future studies should, whenever possible, incorporate longer intervals between playback sequence trials, particularly in populations which are shy and wary.

Distress calls in *M. cataphractus* function as a way of soliciting help when emitted by juvenile crocodile, and as a possible warning to conspecifics when produced by an adult. Understanding these behavioural responses to distress calls, can thus be used to develop improved species monitoring techniques for African slender-snouted crocodiles. As small juvenile distress calls attracted both adult and juvenile *M. cataphractus*, using these signals is likely to produce the best effects in the playback survey monitoring method discussed in Chapter 6.

CHAPTER 6

COMPARING ACOUSTIC AND VISUAL POPULATION MONITORING METHODS FOR ENDANGERED AFRICAN CROCODILE SPECIES

Abstract

Monitoring methods that rely on acoustic communication can provide valuable data for conservation management, and are particularly useful when the animals of interest are vocal but also cryptic, nocturnal, or difficult to access. Crocodilians are very vocal, yet their population monitoring techniques typically involve visual detection of animals using spotlight surveys or aerial counts. These methods are less effective for species that are shy or inhabit densely vegetated wetlands and closed-canopy forests, resulting in limited data on populations of several threatened species, including critically endangered *Mecistops*. To address this problem, I tested the use of passive acoustic monitoring and playback survey for monitoring *Mecistops* spp. in Gabon and Côte d'Ivoire. The acoustic monitoring relied on detecting spontaneous calls emitted by adults during the breeding season, while the playback surveys detect the responses to distress calls. I compared the detection rates obtained through these methods with those from traditional spotlight surveys. In both study sites, passive acoustic monitoring was not successful in detecting crocodile numbers comparable to those obtained through spotlight surveys. Although *Mecistops* were present during all traditional spotlight surveys in Gabon (surveys $n = 17$, 22.8 ± 9.3 km each; detection rate: 0.77 ± 0.56 km^{-1}) and in Côte d'Ivoire (surveys $n = 8$, 8.2 ± 1.4 km each; detection rate: 1.51 ± 0.90 km^{-1}), the acoustic recorders registered only one vocalisation bout in Gabon, and four in Côte d'Ivoire throughout the entire study period. Playback surveys, however, provided significantly higher detection rates than paired spotlight surveys performed on the same nights in both countries, although a higher number of *Mecistops* were detected during playback surveys in Gabon (playback = 3.3 ± 1.4 km^{-1}; spotlight = 1.7 ± 0.5 km^{-1}) than in Côte d'Ivoire (playback = 2.1 ± 1.6 km^{-1}; spotlight = 1.6 ± 0.8 km^{-1}). The use of playback surveys should be incorporated into standard *Mecistops* monitoring protocols to better inform conservation management plans.

6.1 Introduction

Information on distribution and abundance is crucial for management of crocodilians, providing basis for population control, sustainable harvesting, as well as conservation of threatened species (Bayliss, 1987). Monitoring crocodilian population densities is most commonly done using spotlight surveys, a method first developed by Messel and Vorlicek (1981) for *Crocodylus porosus* in the tidal rivers in Northern Australia (Bayliss, 1987; Grigg and Kirshner, 2015). Crocodilians are the only reptiles with retinal tapetum lucidum (Schwab et al., 2002), a reflective layer within the retinal pigment cells which improves night vision by increasing light absorption (Grigg and Kirshner, 2015). This mechanism also causes the light from a torch or spotlight to retro-reflect from the eyes of the crocodile, giving away the animal's position. Spotlight surveys are usually performed at night from a moving boat (Grigg and Kirshner, 2015), though they can also be carried out from land when walking or driving along the shore (Magnusson and Lima, 1991; Simpson, 2006; Grigg and Kirshner, 2015).

Crocodile density is typically expressed as number of animals per km of transect or per km^2 of area surveyed, with the methods standardised to obtain comparable long-term results (Bayliss, 1987). Size class structure of the population is often also monitored, as crocodilian size is a good indicator of its life stage, providing information on population dynamics (Grigg and Kirshner, 2015). However, not all size classes are equally detectable. Young, inexperienced hatchlings are easy to see and to approach, while adult crocodiles are more wary (Ron et al., 1998; Grigg and Kirshner, 2015). Hatchlings also suffer from a high mortality rate of up to 95% (Webb et al., 1983a; Somaweera et al., 2013), thus not all size classes contribute equally to the population (Grigg and Kirshner, 2015).

Although individual spotlight survey protocols need to be adapted to local conditions, their success is affected by the habitat characteristics, as well as species ecology and behaviour. In open, but densely vegetated wetlands and swamps, where land and boat access are limited, daytime aerial counts of individuals or nests from an aircraft or drone have been successfully implemented for population surveys of *C. porosus* (Bayliss, 1987; Magnusson et al., 1980; Evans et al., 2015) and *Crocodylus niloticus* (Ezat et al., 2018). However, aerial surveys are of less use when the target species inhabit and nest in closed-canopy forests, which obstruct the view, or when the target population is composed of shy and wary animals, such as those affected by hunting (Grigg and Kirshner, 2015), as the disturbance caused by the aircraft or drone can affect the sightings (Bevan et al., 2018). Signs of crocodilian presence, such as scat, tracks or slide marks on banks can be used as scores of abundance when sightings of animals are not easily obtained (Simpson, 2006; Grigg and Kirshner, 2015), but they rely on the presence of land, and similarly to traditional spotlight and aircraft surveys, they can be labour-intensive and costly.

Crocodiles from two African genera in need of urgent monitoring and conservation action are found in areas where detection using traditional monitoring methods can be limited. The slender-snouted crocodiles *Mecistops* inhabit remote rivers, wetlands an lakes surrounded by closed-

canopy forest in West and Central Africa (Shirley et al., 2018), and the sympatric African dwarf crocodiles *Osteolaemus* prefer small streams and swamps in the forest interior (Waitkuwait, 1989; Eaton, 2010). The West African slender-snouted crocodile *Mecistops cataphractus* is considered one of the most endangered crocodilians, with few small, severely depleted populations across the Upper Guinea region, the largest of which appears to be in Côte d'Ivoire (Shirley et al., 2018). Central African slender-snouted crocodiles *Mecistops leptorhynchus*, although nationally protected in most countries across their range in Central Africa, have suffered significant declines, with estimated 70% of the remaining global population found in Gabon (Shirley et al., 2018). African dwarf crocodiles *Osteolaemus* spp., although reported to be widespread and locally abundant throughout most of their range (Eaton, 2010), have received little attention through targeted surveys and after a recent taxonomic split (Eaton et al., 2009) are awaiting species revalidation/description and a conservation assessment update (Crocodile Specialist Group, 1996; Eaton, 2010; Smolensky, 2015). Both genera are affected by the bushmeat trade, hunting, habitat loss and subsistence fishing (Eaton, 2010; Shirley, 2014; Shirley et al., 2018), resulting in small, fragment populations of shy, cryptic animals. However, both genera are also reported to be highly vocal, particularly during the breeding season (Dinets, 2013b; Shirley et al., 2018), providing potential for incorporating crocodilian acoustic ecology into population monitoring of the species.

There are several wildlife monitoring methods that rely on sound. These include: passive acoustic monitoring, which employs acoustic sensors to record naturally occurring sounds over time (Blumstein et al., 2011; Browning et al., 2017); active acoustic monitoring, involving detection of sound-emitting devices, such as animal tags (Stein, 2011); as well as playback surveys and lure counts, which incorporate broadcasting a sound to elicit a response or attract the animals, which can then be counted (Allen et al., 2004; Hill and Greenaway, 2005). Active acoustic monitoring, which has been applied to crocodilians in the past (Rosenblatt and Heithaus, 2011; Dwyer et al., 2015), requires capture of target animals, with the data collection focused on movement and behaviour of the tagged individuals, rather than on population size and structure. Passive acoustic monitoring provides a non-invasive tool for wildlife monitoring and is particularly suited for vocal species that are shy, cryptic and for habitats with limited visibility or access (Blumstein et al., 2011; Wrege et al., 2017). Although never used on crocodilian populations before, acoustic monitoring can provide data on animal presence, behavioural ecology, population density and structure, as with birds (Digby et al., 2013; Frommolt and Tauchert, 2014; Sanders and Mennill, 2014), bats (Bader et al., 2015), cetaceans (Mellinger et al., 2007; Klinck et al., 2012), elephants (Wrege et al., 2017), amphibians (Weir et al., 2009; Stevenson et al., 2015), insects (Chesmore and Ohya, 2004), and fishes (Nordeide and Kjellsby, 1999; Lobel, 2002). Playback surveys and lure counts also enable detection of otherwise elusive, nocturnal or rare animals, and while not applied to crocodilians before, they have been used in monitoring bats (Hill and Greenaway, 2005), birds (Allen et al., 2004; Vrezec and Bertoncelj, 2018), primates (Bryant et al., 2016), koalas (Jurskis et al., 2001) and large mammalian predators (Mills et al., 2001; Omoya et al., 2014).

In this chapter, I test the use of passive acoustic monitoring and playback surveys as new methods for monitoring the threatened African crocodiles, with particular focus on the critically endangered *Mecistops* spp., and compare the detection rates obtained through these systems with those from traditional spotlight surveys. Crocodilians produce a range of airborne and underwater sounds throughout all stages of their lives (Vergne et al., 2009). The passive acoustic monitoring relied on detecting spontaneous vocalisations emitted by adult crocodiles as part of courtship and territory defence (Garrick and Lang, 1977; Shirley et al., 2018) during the breeding season. Adults are generally long-lived, have long reproductive lives and few natural predators, thus serving as population source (Somaweera et al., 2013; Grigg and Kirshner, 2015) and of primary interest for population monitoring and conservation management. All crocodilians are semi-aquatic, and the adults are often partially submerged when producing calls (Vliet, 1989; Wang et al., 2007), resulting in sound being transmitted through both air and water. As sound waves travel further through the water (Bradbury and Vehrencamp, 2011), potentially allowing for a larger detection range than when monitoring airborne sound only, I used both underwater and aerial sensors to record wild crocodile vocalisations. Crocodiles also use distress calls to warn and solicit help from conspecifics, and *M. cataphractus* can respond to distress calls by approaching the source of the call (Chapter 5; Shirley et al., 2018). By incorporating broadcasts of distress calls into a spotlight survey, I test whether the use of playback increased the detectability of crocodiles. Improving detection rates can provide better estimates for population density and size, informing future conservation efforts for the species.

6.2 Methods

6.2.1 Study sites

In order to maximise the chances of obtaining sufficient detection sample sizes for the different monitoring techniques, I tested the passive acoustic recorders in two sites with relatively large reported populations of *Mecistops* (Shirley et al., 2018): the Bongo River region of the Gamba Complex in Gabon (−2.432000, 10.132291), and the Hana River at the south-western edge of the Taï National Park in Côte d'Ivoire (5.389406, −7.25214). I tested the playback survey along the Hana River in and outside Taï National Park. Detailed study site descriptions are presented in Chapters 2 and 3.2.

Additional playback survey data used in the analysis were collected by Matt Shirley on the Ngowe and Echira Rivers in the Akaka region of Loango National Park in Gabon (−2.22776, 9.68744; Fig. 6.1) between 8–22 November 2010. The rivers were surrounded by extensive swamps with dense floating vegetation, including grass and papyrus, as well as flooded forest, and were inhabited by two crocodilian species: *M. leptorhynchus* and *Osteolaemus tetraspis* (Matt Shirley, pers. comm.).

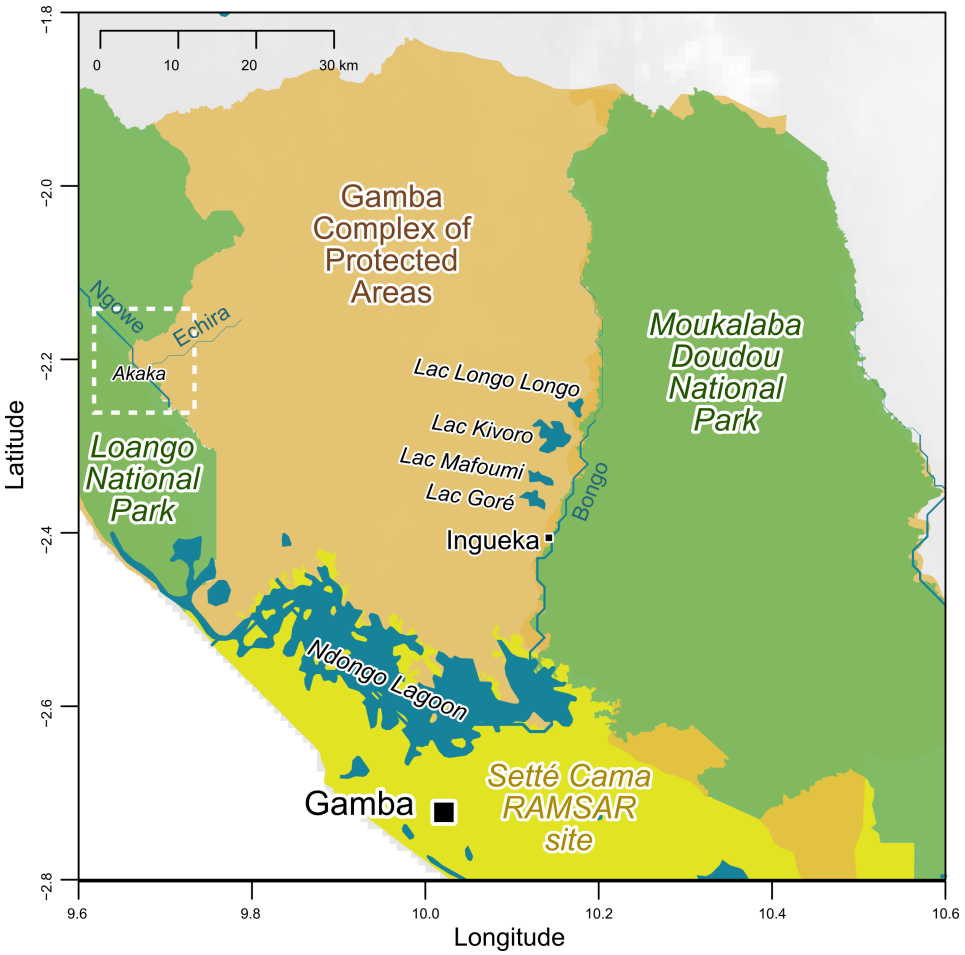

FIGURE 6.1. The Gamba Complex of Protected Areas, including Moukalaba-Doudou and Loango National Parks, and the Sette Cama RAMSAR site (IUCN and UNEP-WCMC, 2018). White dashed lines mark the study site in the Akaka region.

6.2.2 Spotlight surveys

To assess the encounter rates of crocodiles in the locations where acoustic monitoring took place, I carried out spotlight surveys from a motor boat over the same study period. Each location was surveyed at least twice, on different nights. In the Bongo River region, I carried out 17 surveys between 24 January and 23 February 2018 (22.8 ± 9.3 km each), surveying the lagoon (five nights, 24.6 ± 6.4 km each), the lakes (8 nights, 19.7 ± 9.9 km each) and the river (4 nights, 27.0 ± 11.1 km each). In the south-western Taï National Park, I carried out eight spotlight surveys between 14 April and 12 May 2018 (8.2 ± 1.4 km each), including six nights surveying the park border (8.3 ± 1.5 km each), and two nights in the park interior (7.8 ± 1.4 km each). An additional four surveys were carried out on the Hana and Meno Rivers outside of the protected area (11.7 ± 3.2 km each), however, due to the high risk of equipment theft, acoustic recorders were not installed in that section of the river.

Upon spotting a crocodile, I identified it to species or marked as eyes-only (EO) and logged its position using a Garmin GPSMap 64s handheld recorder. Where possible, I estimated the animal's size and categorized it into one of three size classes: hatchling/small juvenile (< 60 cm total body length), large juvenile/subadult (60–200 cm total body length), adult (> 200 cm total body length). Adult *Osteolaemus* spp. were included in the juvenile/subadult size class.

6.2.3 Acoustic monitoring

Before commencing the acoustic recording, I carried out preliminary spotlight surveys in the study sites (Bongo River region on 24–25 January 2018; south-western Taï National Park area on 14 April 2018) in order to confirm the presence of crocodiles and select recording locations with suitable trees for recorder and hydrophone installation (Fig. 6.2).

To record the acoustic activity in the study area, I used two recording units at a time. Each unit comprised of one underwater and one aerial recorder. Aerial sounds were recorded using a custom-built SOLO recorder after Whytock and Christie (2017), composed of a Raspberry Pi model A+, Creative SoundBlaster Play 3 sound card, PiFace shim RTC clock, ETC Technology 24,000 mAh powerbank, all encased in a weatherproof DRiBOX 200, and connected to one Primo EM172 microphone; see Whytock and Christie (2017) for details on the recorder construction and set up. Underwater sounds were recorded with a commercially available Wildlife Acoustics Song Meter 2+ (SM2+), connected to two HTI-95 hydrophones with 20 m long cables for stereo underwater sound recording.

Both recorders were installed next to each other, attached to a tree near or at the shore, 1.5–2 m above the water level, with the hydrophones placed in the water at a depth of 50–80 cm, positioned at a distance of 11.4 ± 4.3 m relative to each other (Fig. 6.2). All distances were measured using a Shotsaver S400 laser range finder. The hydrophones were attached to tree branches, roots, or other fixed features in the water, to ensure their position did not change throughout the monitoring period. Each monitoring unit was placed at one location for three days, and set to record continuously for 72 hours. After the three days, the units were moved to the next location in the study area. The recorders were tested before the first day of recording to ensure optimal settings configuration (see Appendix B).

In Bongo River area, I installed acoustic monitoring units in 18 locations: six in the lagoon, six in the lakes, and six along the river (Fig. 6.3, Table 6.1). In south-western Taï National Park, I installed acoustic monitoring units in 13 locations: seven on the border of the Park, five on the river inside the Park, and one in the forest interior of the Park (Fig. 6.4, Table 6.2). Due to rapid flooding on 21 April 2018 after heavy rains in Taï National Park interior, one of the SM2+ recorders was damaged, resulting in no subsequent underwater recordings in three park interior sites and one of the park border sites (Table 6.2).

FIGURE 6.2. Examples of the acoustic recorder installations in the field: SOLO recorder in a black weatherproof box attached to a tree branch (A), Wildlife Acoustics SM2+ (green box) attached to a tree branch, with hydrophone cables routed along the branches (B).

TABLE 6.1. Details of recorder locations in the Bongo River region: habitat type and recorder number, recording dates, GPS coordinates, distance between the two hydrophones, water level and water flow (rated between 0–4, where 0 denotes no visible water movement, and 4 denotes strong flow).

Habitat	Site	Recording dates	GPS location (decimal degrees)	Hydrophone distance (m)	Water level (m)	Water flow (0–4)
Lagoon	1	12–15 Feb	−2.54509,10.12553	8.0	1.3	2
	2	15–18 Feb	−2.52706,10.08876	8.4	0.9	0
	3	18–21 Feb	−2.51060,10.08022	11.7	1.5	0
	4	18–1 Feb	−2.52236,10.11055	8.3	0.6	2
	5	21–24 Feb	−2.54066,10.09748	5.4	1.2	0
	6	21–24 Feb	−2.56491,10.11583	4.0	0.9	0
Lake	1	26–29 Jan	−2.24908,10.18058	17.1	2.1	1
	2	30 Jan–2 Feb	−2.37105,10.14956	11.0	2.0	0
	3	30 Jan–2 Feb	−2.38182,10.14783	17.0	2.4	1
	4	2–6 Feb	−2.35968,10.13656	12.7	1.3	1
	5	6–9 Feb	−2.25645,10.18321	8.0	1.0	0
	6	9–12 Feb	−2.23760,10.20048	12.1	2.2	0
River	1	26–29 Jan	−2.31612,10.18335	16.1	3.0	4
	2	2–6 Feb	−2.33671,10.17922	14.4	4.0	4
	3	6–9 Feb	−2.27990,10.17714	10.2	4.0	4
	4	9–12 Feb	−2.26041,10.19650	18.4	4.0	4
	5	12–15 Feb	−2.53388,10.13969	16.3	2.5	4
	6	15–18 Feb	−2.52773,10.12686	6.4	5.0	3

6.2.4 Playback surveys

I performed the playback surveys in Côte d'Ivoire, along the Hana and Meno rivers, on six nights between 25 April and 12 May 2018, following a methodology used in the Akaka region, Gabon in 2010 (Matt Shirley, pers. comm.). During each night of the playback, I surveyed a 10.0 ± 2.8 km section of the river in one of the three areas: inside the Taï National Park, along its border, or outside of the protected zone (Fig. 6.5). I travelled by boat along the river, and stopped at 400 m intervals (14 ± 2 points per survey, 86 points in total). At each stopping point, I played three *M. cataphractus* distress call sequences—one of a small juvenile, one of a large juvenile, and one of an adult—in a randomised order, with 30 s of silence between each sequence; see Chapter 5 for details on the call sequences and playback procedure. Two observers monitored the river with spotlights and I noted down the numbers and behaviour of crocodiles visible before, during, and after each playback sequence. Any additional crocodiles (identified to species and EO) spotted with the spotlight when travelling between the playback points were added to the number of animals encountered during the playback survey.

Each river section was surveyed twice, on different nights, with the playback survey performed either on the way forward from camp, or on the return journey. As a control, on each night of

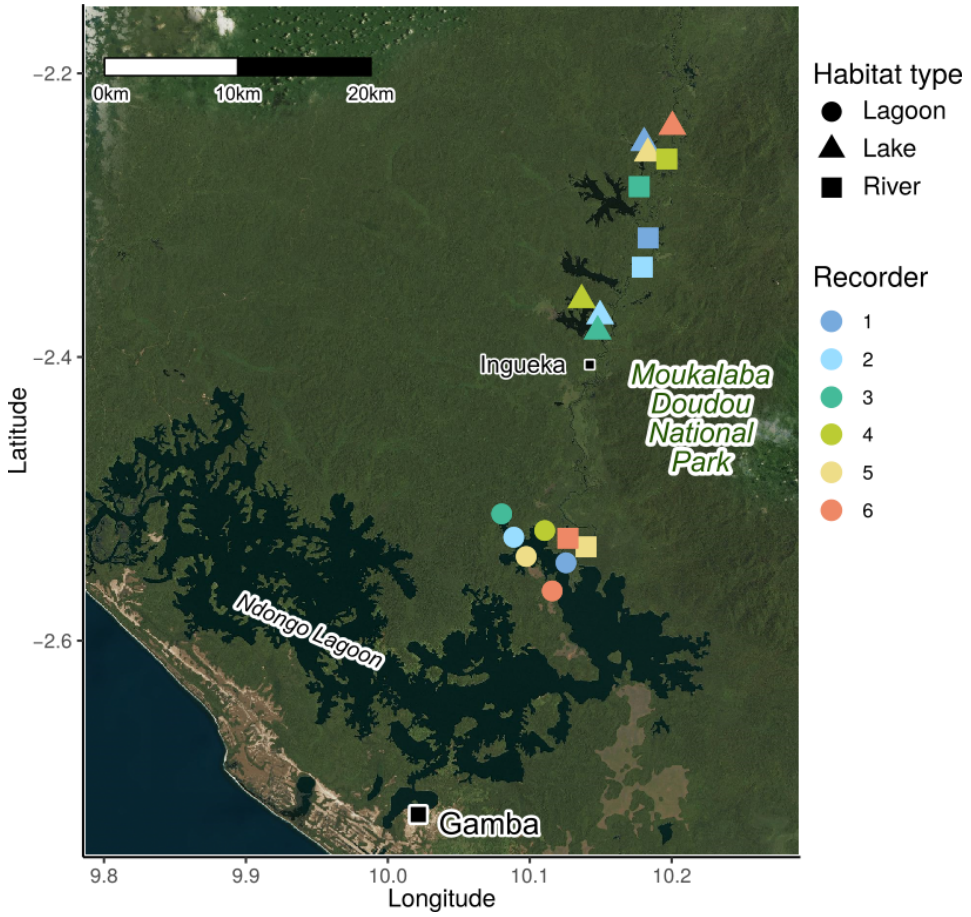

FIGURE 6.3. Locations of the recording units in the Bongo River area, divided into the three habitat types: lagoon (six recording locations), lake (six recording locations) and river (six recording locations). Base map: Bing Map Aerial.

playback, I also performed a spotlight-only survey on the same section of the river, in the direction opposite to that of the playback survey that night, and counted all crocodiles (identified to species and EO) encountered.

In the Akaka region, the playback surveys were performed along three river sections: Echira River (9.1 ± 1.3 km), Ngowe River upstream from the Echira River mouth (10.3 ± 0.8 km), and Ngowe River downstream from the Echira River mouth (10.0 ± 0.0 km) (Fig. 6.6). Each section was surveyed twice, on different nights, between 8–22 November 2010. During the playback surveys, distress call sequences of hatchling, juvenile and adult *M. leptorhynchus* recorded locally were played using RadioShack Mini Audio Amplifier, with playback points at 500 m intervals along the river section (Matt Shirley, pers. comm.). Each playback survey contained 15 ± 2 playback points, with 90 points in total. Crocodiles visible before, during and after each playback sequence were recorded, as well as the numbers of vocal responses to the playback sequences. To avoid pseudo-replication, multiple vocal responses to playback sequence of crocodiles not visible to the

TABLE 6.2. Details of recorder locations on the Hana River in south-western Taï National Park: habitat type and recorder number, recording dates, GPS coordinates (decimal degrees), distance between the two hydrophones, water level and water flow (rated between 0–4, where 0 denotes no visible water movement, and 4 denotes strong flow). Sites with no underwater recorders are marked with an asterisk.

Habitat	Site	Recording dates	GPS location (decimal degrees)	Hydrophone distance (m)	Water level (m)	Water flow (0–4)
Border	1	13–16 Apr	5.413083,−7.24248	6.0	1.2	3.5
	2	13–16 Apr	5.417000,−7.23917	7.2	1.4	4
	3	19–22 Apr	5.415483,−7.24197	9.1	0.7	2
	4	19–22 Apr	5.393683,−7.25292	6.0	0.8	3
	5	30 Apr–3 May	5.407417,−7.24527	7.2	1.7	3
	6*	30 Apr–3 May	5.399983,−7.24933	n/a	0.4	1
	7	7–10 May	5.399367,−7.25180	10	1.3	3
Park (river)	1	16–19 Apr	5.419817,−7.22488	6.0	0.9	4
	2	16–19 Apr	5.413467,−7.23130	10.1	1.6	3
	3*	22–25 Apr	5.42685,−7.21313	n/a	2.4	3.5
	4*	27–30 Apr	5.430033,−7.21230	n/a	0.9	4
	5	27–30 Apr	5.42440,−7.21945	7.0	2.1	4
Park (forest)	1*	7–10 May	5.412217,−7.24135	n/a	0.4	0

observer were considered to be a single responding animal in the analysis.

6.2.5 Analysis

6.2.5.1 Acoustic analysis

I used SASLAB PRO 5.2.12 (Avisoft Bioacoustics, 2017) to manually identify crocodile vocalisations on spectrograms in all of the recordings, examining each file twice. To identify the crocodile vocalisations, I used the *O. tetraspis* call recordings presented in Chapter 4, as well as recordings of 29 vocalisations from a pair (male and female) of *M. cataphractus* filmed at the St. Augustine Alligator Farm Zoological Park (Matt Shirley, pers. comm.) as a reference (Table 6.3). These could be classified into several different types, including "long growls" (n = 7), "booming roars" (n = 12) (Shirley et al., 2018, Fig. 6.7), as well as possible third type of shorter roars (n = 10). I used SEEWAVE (Sueur et al., 2008) (FFT length = 1,024, window = Hanning, overlap = 99%, bandwidth 0–5 kHz) to calculate the maximal (dominant) frequency, and PRAAT 6.0.43 (Boersma and Weenink, 2018) to measure the call duration and extract the mean pitch (fundamental frequency), from the narrow-band (0–2 kHz) signal spectrogram following Chabert et al. (2015). Due to differences in recording quality and temporal overlap of many of the calls recorded in captivity, I only measured the acoustic parameters of the calls that were clear and did not overlap in time with another call ("long growl" n = 3, "booming roar" n = 2).

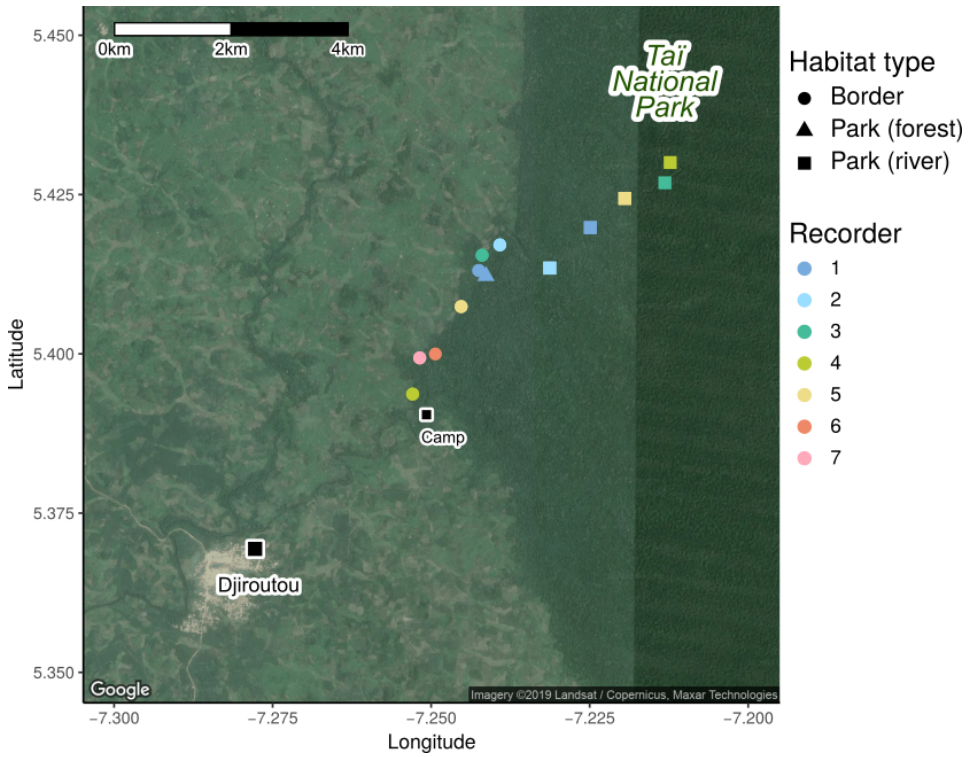

FIGURE 6.4. Locations of the recording units in the south-western Taï National Park, divided into the three habitat types: National Park border (seven recording locations), forest inside the National Park (one recording location), and river inside the National Park (five recording locations). Base map: Google Satellite.

6.2.5.2 Statistical analysis

All statistical analyses were performed using R 3.6.0 (R Core Team, 2018). To compare the crocodile encounter rates during spotlight surveys between the different habitat types, I used a one-way ANOVA for the data collected in the Bongo River region. As the residuals of encounter rates in different sections of the river in south-western area of Taï National Park were not normally distributed, I used the non-parametric Kruskal-Wallis test to compare them. To determine the effectiveness of playback surveys versus spotlight-only surveys, I used a paired *t*-test, comparing the numbers of crocodiles encountered during the playback with the numbers encountered during a spotlight-only survey on the corresponding night.

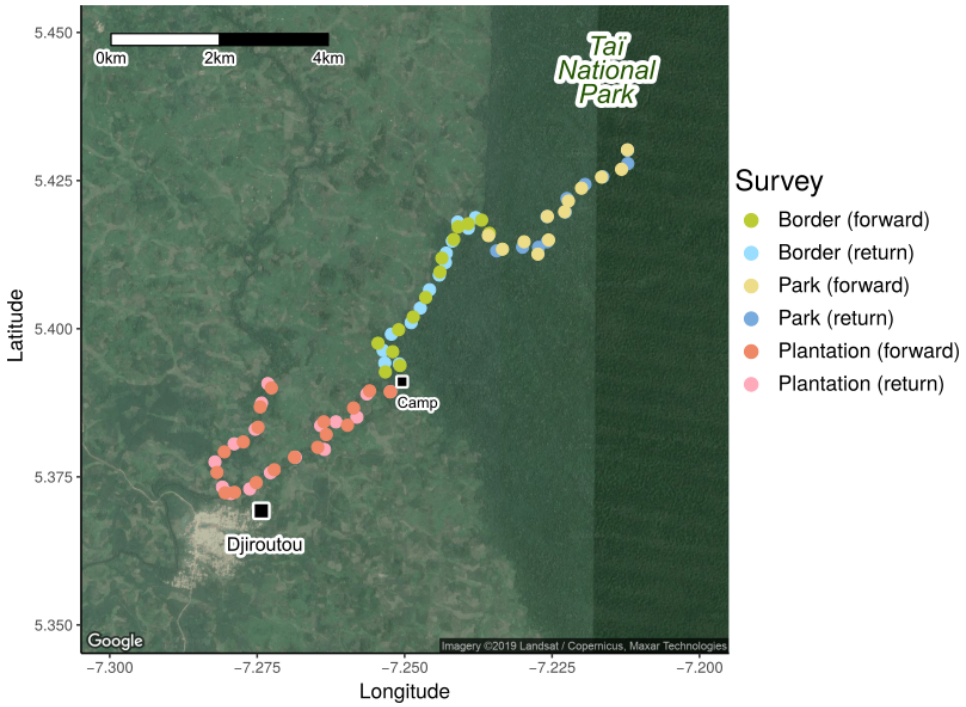

FIGURE 6.5. Locations of the playback survey points in the south-western area of Taï National Park. Forward and return directions are relative to the Camp position. Base map: Google Satellite.

6.3 Results

6.3.1 Spotlight surveys vs passive acoustic monitoring

6.3.1.1 Bongo River region

Spotlight surveys revealed crocodiles present in all three habitat types monitored (Fig. 6.8): the river (encounter rate = 1.36 ± 0.8 km^{-1}), the lakes (encounter rate = 1.25 ± 0.77 km^{-1}), and the lagoon (encounter rate = 2.11 ± 0.89 km^{-1}). General crocodile encounter rates were not significantly different between the three habitat types ($F_{2,14} = 1.779$, $P = 0.205$).

Species distribution varied with the habitat types (Fig. 6.9; also see Chapter 3). In all three habitats *M. leptorhynchus* was the most frequently encountered crocodilian (lagoon = 1.08 ± 0.52 km^{-1}; lake = 0.58 ± 0.47 km^{-1}; river = 0.77 ± 0.75 km^{-1}). *Osteolaemus tetraspis* was rarely sighted in all three areas, (lagoon = 0.04 ± 0.04 km^{-1}; lake = 0.06 ± 0.05 km^{-1}; river = 0.11 ± 0.08 km^{-1}), while *C. niloticus* was found primarily in the lagoon (0.27 ± 0.13 km^{-1}), with few individuals spotted in the river (0.01 ± 0.01 km^{-1}). Of the 665 crocodiles encountered during the spotlight surveys, 249 (37%) were recorded as eyeshine only (EO). The rates of encounter with crocodiles not identified to species were not significantly different between the three habitat types ($F_{2,14} = 0.538$, $P = 0.595$; Fig. 6.9). Among the 290 *M. leptorhynchus* identified, 73.8% of sightings were of larger

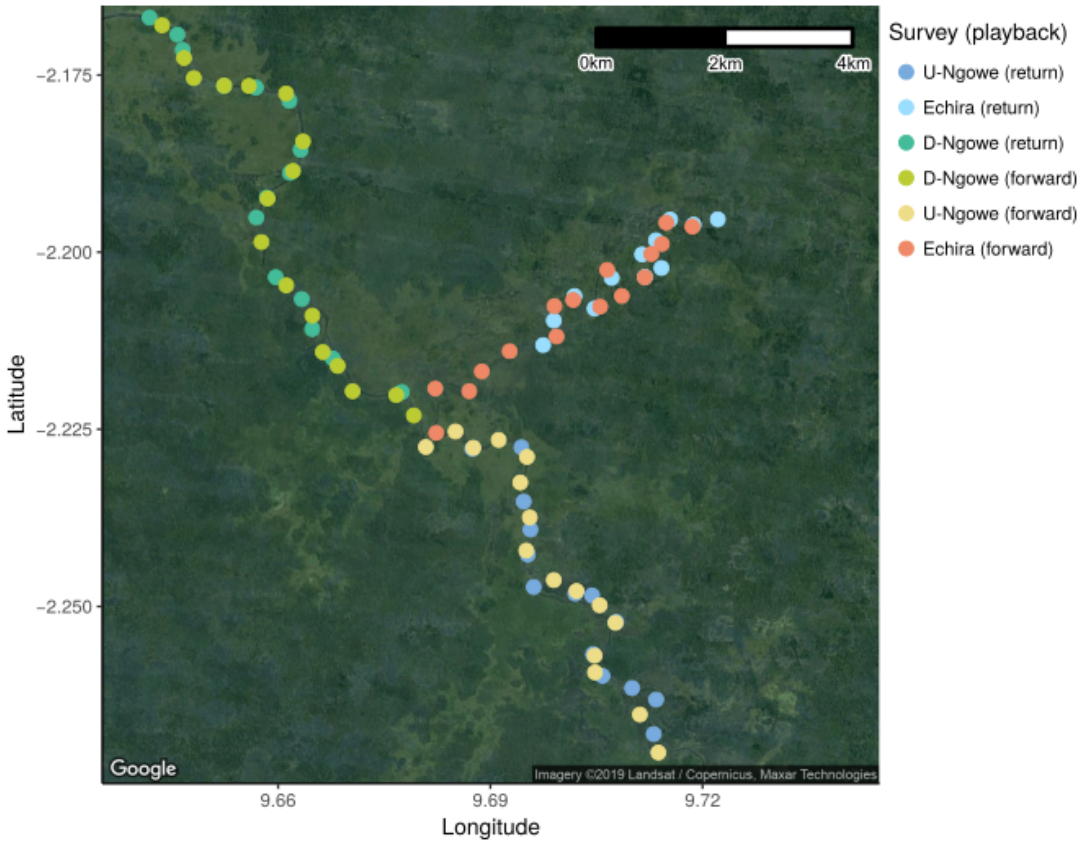

FIGURE 6.6. Locations of the playback survey points in the Akaka region of Loango National Park in three river sections: upstream Ngowe River (U-Ngowe), downstream Ngowe River (D-Ngowe), and on Echira River. Forward and return directions are relative to the centre of the map (Matt Shirley, pers. comm.). Base map: Google Satellite.

juveniles/subadults (60–200 cm total length), 21.4% were smaller juveniles (< 60 cm total body length), while 4.8% were adults (> 200 cm total length). Of the 35 identified *C. niloticus*, 65.7% were smaller juveniles, 28.6% were larger juveniles/subadults, and 5.7% were adults (Fig. 3.6).

In the 1,296 h recorded in total over all the recording sites, there were two suspected crocodile vocalisation bouts recorded during the study period. On 10 February 2018 at 0251 hours, there were four drums recorded (Table 6.3), probably produced by *O. tetraspis* (Fig. 6.10A). On 12 February 2018 at 0522 hours, there were two long growls recorded (Table 6.3), likely produced by *M. leptorhynchus* (Fig. 6.10B). Both vocalisation bouts were recorded in the same location (Lake-6; Fig. 6.3), and registered on the aerial recorder only. There were no underwater crocodile vocalisations recorded.

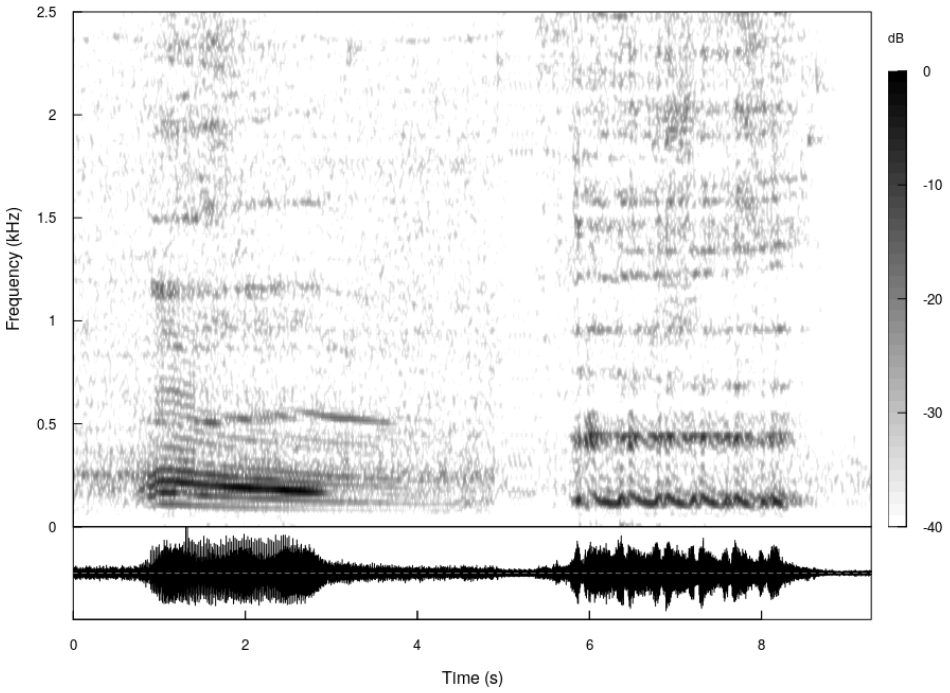

FIGURE 6.7. Composite spectrogram with examples of two types of calls emitted by captive *M. leptorhynchus* during a calling duet, recorded at St. Augustine Alligator Farm Zoological Park (Matt Shirley, pers. comm.). The first vocalisation was referred to as a "long growl", and the second as a "booming roar" (Shirley et al., 2018). Original video source: https://www.youtube.com/watch?v=msn0xp1iKJ0 (Accessed 18 August 2019). Sampling rate 16,000 Hz, FFT size 1,024, Hanning window, overlap 93.75.

TABLE 6.3. Acoustic characteristics (mean ± SD) of the vocalisations recorded during the acoustic monitoring in the Bongo River region (Bongo) and Taï National Park (Taï), as well as the confirmed adult *M. cataphractus* vocalisations recorded at St. Augustine Alligator Farm Zoological Park (Zoo). Dominant (max.) frequency refers to the mean dominant frequency of the call.

Call type	**Location**	**Species**	***n***	**Duration (s)**	**Max. Frequency (Hz)**	**Mean Pitch (Hz)**
Drums	Bongo	*O. tetraspis*	4	0.16 ± 0.03	31.46 ± 0.05	n/a
Long growl	Bongo	*M. leptorhynchus*	2	2.93 ± 1.30	402 ± 61	125 ± 45
Long growl	Taï	*M. cataphractus*	12	2.06 ± 0.83	158 ± 57	167 ± 17
Long growl	Zoo	*M. cataphractus*	3	3.21 ± 0.54	189 ± 1	193 ± 10
Booming roar	Zoo	*M. cataphractus*	2	2.53 ± 0.21	125 ± 3	–

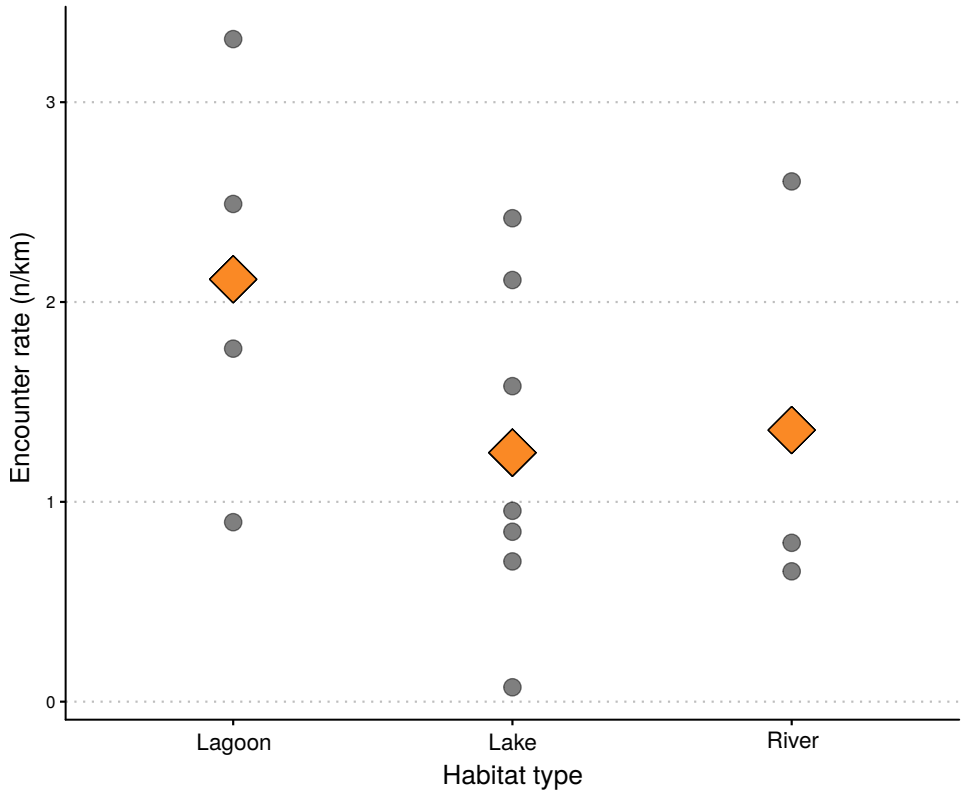

FIGURE 6.8. Total crocodile encounter rates during spotlight surveys (n) in the three habitat types in Bongo River area: lagoon ($n = 5$), lake ($n = 8$), and river ($n = 4$). The grey dots represent individual surveys. The orange diamonds represent the mean encounter rate per habitat type.

6.3.1.2 South-western Taï National Park

Crocodiles were encountered on all nights of the spotlight surveys in the areas where acoustic monitoring was deployed (Fig. 6.11): Hana River flowing through the Taï National Park interior (encounter rate = 2.57 ± 0.74 km^{-1}) and forming the park border (encounter rate = 2.66 ± 0.99 km^{-1}). Crocodiles were also encountered during spotlight surveys outside of the protected area (encounter rate = 0.79 ± 0.41 km^{-1}), where acoustic recorders were not installed. The rates of encounter were significantly lower outside of the protected area, than along the border or inside the National Park (Kruskal-Wallis $\chi^2 = 7.385$, df = 2, $P = 0.025$; Fig. 6.11).

The majority of crocodiles identified to species were *M. cataphractus* (see Chapter 3), encountered in all three sections of the river (park border = 1.92 ± 0.71 km^{-1}; park interior = 2.02 ± 1.09 km^{-1}; plantation = 0.64 ± 0.45 km^{-1}). *Osteolaemus* aff. *tetraspis* was rarely encountered along the river (park border = 0.02 ± 0.05 km^{-1}; park interior = 0.13 ± 0.02 km^{-1}; plantation = 0.04 ± 0.05 km^{-1}). Of the 636 crocodiles encountered throughout the surveys, 217 (34%) were recorded as eyeshine only (Fig. 6.12). Among the 125 *M. cataphractus* identified (Fig. 3.12), 70.4% of sightings

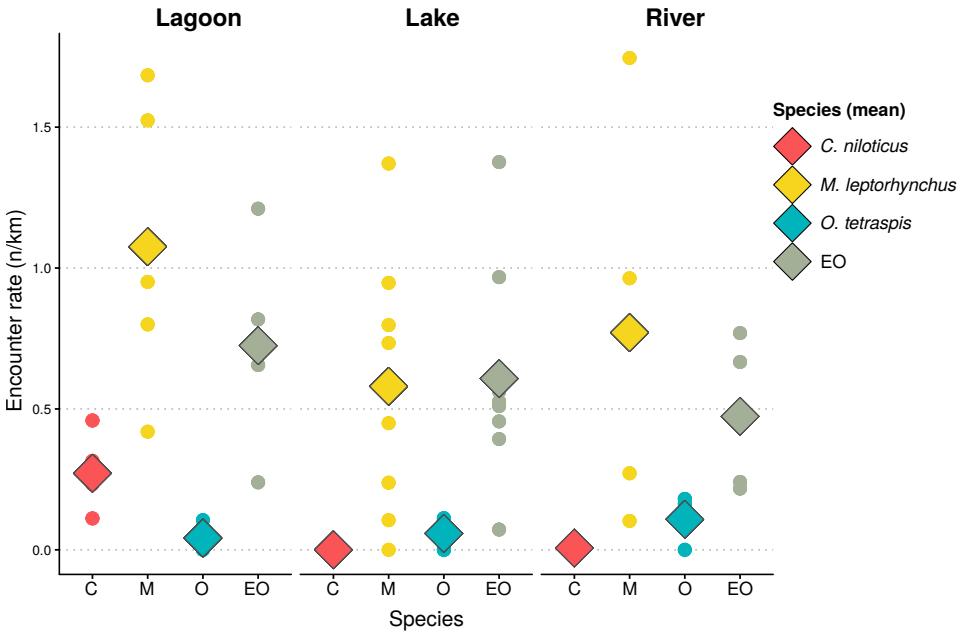

FIGURE 6.9. Encounter rates of *C. niloticus* (C), *M. leptorhynchus* (M), *O. tetraspis* (O) and eyeshine only (EO) during spotlight surveys (n) in the three habitat types in Bongo River area: lagoon ($n = 5$), lake ($n = 8$), and river ($n = 4$). The dots represent individual surveys, the diamonds represent the mean.

were of larger juveniles/subadults (60–200 cm total length), 19.2% were smaller juveniles (< 60 cm total body length), while 10.4% were adults (> 200 cm total length).

In the 914 h recorded in total over all the recording sites, there were four vocalisation bouts, with a total of 14 individual crocodile vocalisations recorded during the study period (Table 6.3). All vocalisations recorded are suspected to be *M. cataphractus*. On 18 April 2018 at 1332 hours, there were two vocalisation bouts, each lasting 22.0 ± 1.1 s, and each composed of four calls (Fig. 6.13). Two more vocalisation bouts, each lasting 9.3 ± 0.3 s and each composed of three calls, were recorded on 19 April 2018 at 0021 hours. Both recordings were at the same location, along the Hana River in Taï National Park interior (Park-River-2, Fig. 6.4). The calls were only registered on the microphone, with no underwater crocodile vocalisations recorded.

6.3.2 Spotlight surveys vs playback surveys

The playback surveys revealed significantly higher numbers of crocodiles than spotlight-only surveys ($t = -4.201$, $\mathrm{df} = 11$, $P = 0.001$), with a higher or equal number of crocodiles encountered during the playback compared to the corresponding spotlight-only survey on the same night (Table 6.4). In the Akaka region of Loango National Park, during the playback surveys there was a significant 199% increase in the total number of crocodiles encountered ($t = -4.711$, $\mathrm{df} = 5$, $P = 0.005$), compared to spotlight-only surveys (encounter rate playback = 3.3 ± 1.4 km^{-1};

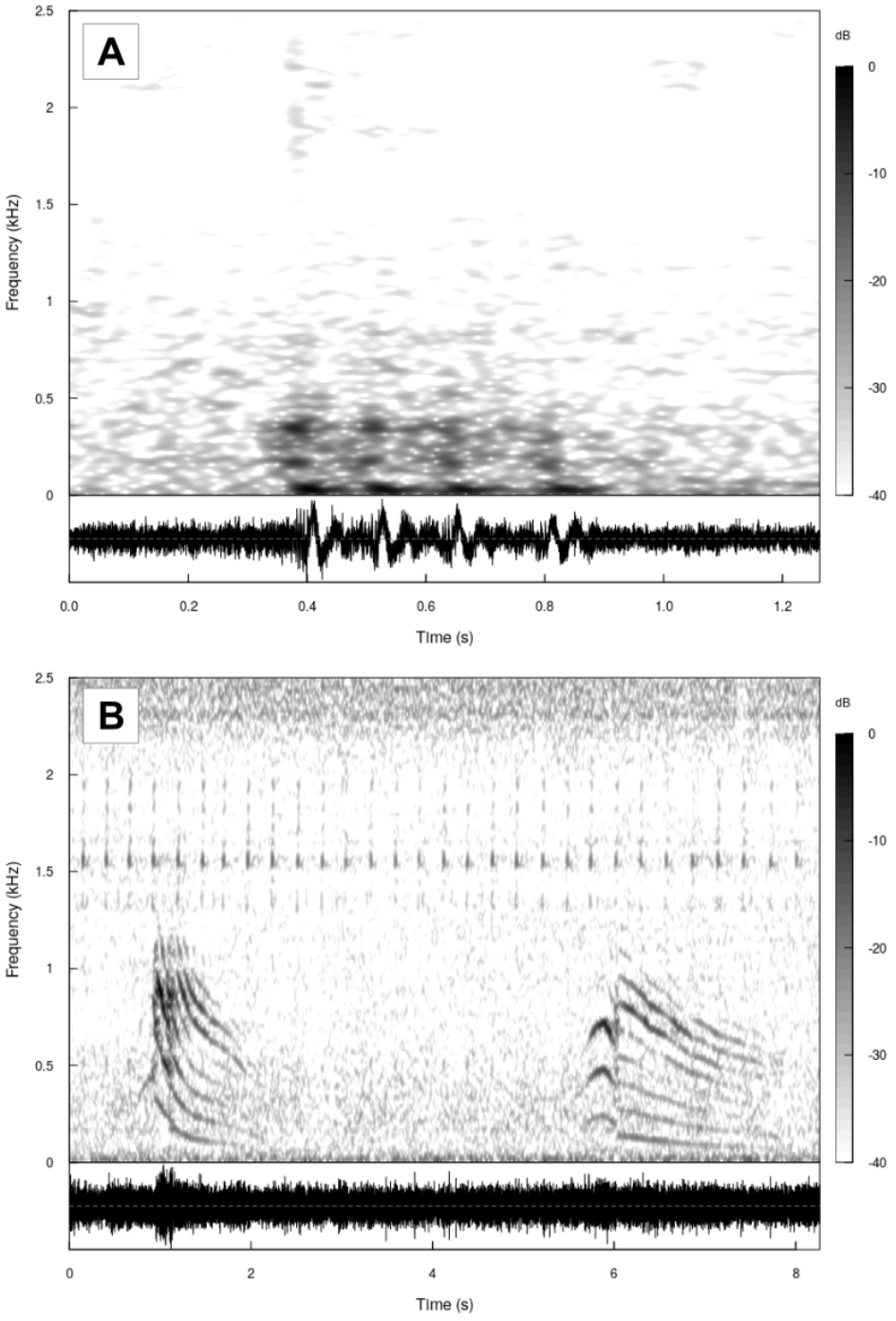

FIGURE 6.10. Suspected *O. tetraspis* drums (A) and *M. leptorhynchus* calls (B) recorded in the Bongo River region during acoustic monitoring. Sampling rate 8 kHz, FFT size 1,024, Hanning window, overlap 93.75.

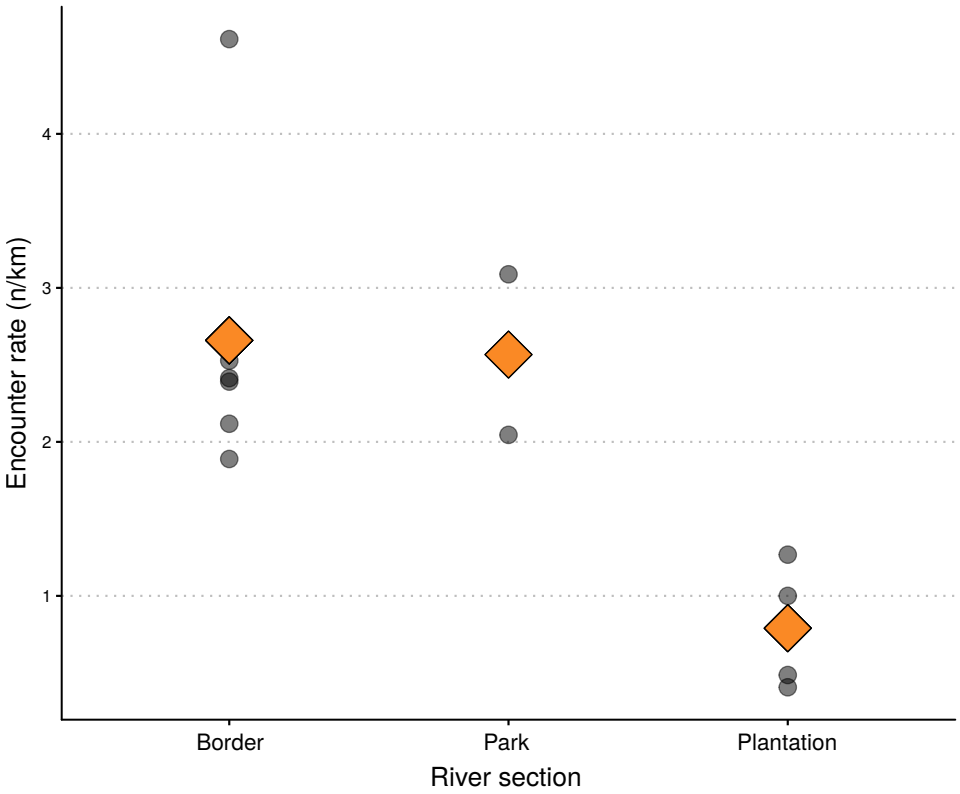

FIGURE 6.11. Total crocodile encounter rates during spotlight surveys (n) in the three river section in south-western Taï National Park area: park border ($n = 6$), park interior ($n = 2$), and plantation ($n = 4$). The grey dots represent individual surveys. The orange diamonds represent the mean encounter rate per habitat type.

encounter rate spotlight-only = 1.7 ± 0.5 km^{-1}). In south-western Taï National Park, the playback surveys also revealed a significantly higher number of crocodiles, compared to the corresponding spotlight-only surveys ($t = -2.690$, df $= 5$, $P = 0.043$), with a 134% increase in encounters during the playback surveys (encounter rate playback = 2.1 ± 1.6 km^{-1}; encounter rate spotlight-only = 1.6 ± 0.8 km^{-1}). Of the total 118 crocodiles detected during the playback surveys in Taï National Park, 75 (64%) were identified as *M. cataphractus*, and 43 (36%) as EO. No *O.* aff. *tetraspis* were identified during the playback surveys.

6.4 Discussion

Spotlight surveys were more successful at detecting crocodile presence than the passive acoustic monitoring, with *Mecistops* spp. having the highest rates of encounter among crocodilians in both study sites. However, playback surveys allowed for detection of even greater numbers of crocodiles, and particularly so for *Mecistops*, than the spotlight-only surveys.

Although crocodiles were found in all monitored habitats, the passive acoustic monitoring

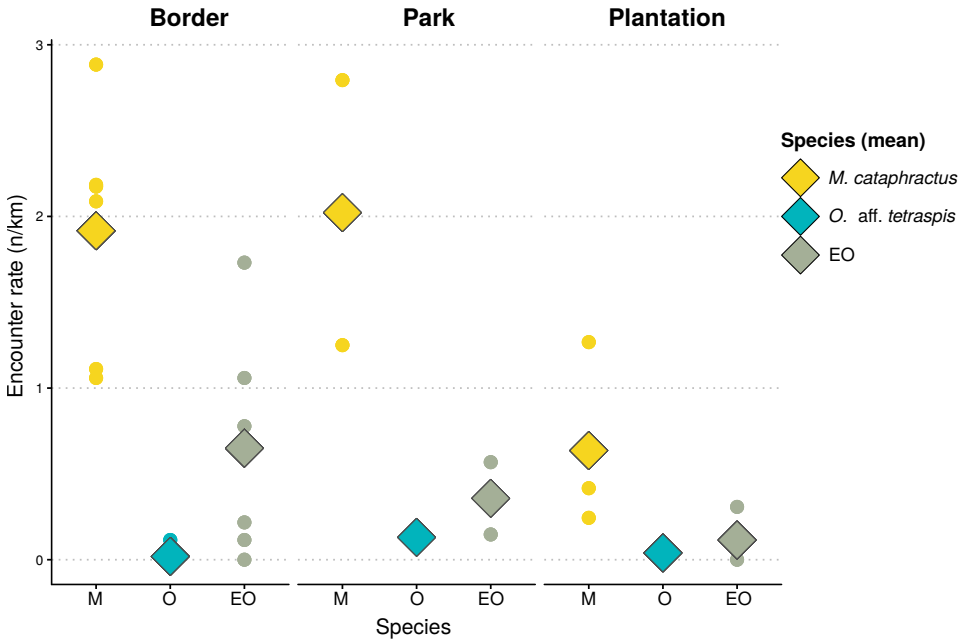

FIGURE 6.12. Encounter rates of *M. cataphractus* (M), *O.* aff. *tetraspis* (O) and eyeshine only (EO) during spotlight surveys (n) in the three river section in south-western Taï National Park area: park border ($n = 6$), park interior ($n = 2$), and plantation ($n = 4$). The dots represent individual surveys, the diamonds represent the mean.

TABLE 6.4. Crocodiles encountered during the playback surveys and during the corresponding spotlight-only surveys in the three river sections of Taï National Park (border, park and plantation), and three river sections of the Akaka region (Echira, D-Ngowe, U-Ngowe).

Section	**Direction**	**Date**	**Distance (km)**	**Playback crocodiles n (n km^{-1})**	**Spotlight crocodiles n (n km^{-1})**
Border	Forward	5 May 2018	9.0	29 (3.2)	17 (1.9)
Border	Return	25 Apr 2018	8.7	21 (2.4)	21 (2.4)
Park	Forward	12 May 2018	6.8	24 (3.4)	16 (2.4)
Park	Return	28 Apr 2018	8.8	20 (2.3)	17 (1.9)
Plantation	Forward	9 May 2018	12.3	7 (0.6)	5 (0.4)
Plantation	Return	1 May 2018	14.3	13 (0.9)	9 (0.6)
Echira	Forward	22 Nov 2010	10.6	27 (2.6)	17 (1.8)
Echira	Return	9 Nov 2010	8.0	34 (4.3)	12 (1.5)
D-Ngowe	Forward	19 Nov 2010	10.0	38 (3.8)	18 (1.8)
D-Ngowe	Return	13 Nov 2010	10.0	52 (5.2)	25 (2.5)
U-Ngowe	Forward	21 Nov 2010	11.5	18 (1.6)	9 (0.9)
U-Ngowe	Return	8 Nov 2010	10.0	22 (2.2)	15 (1.5)

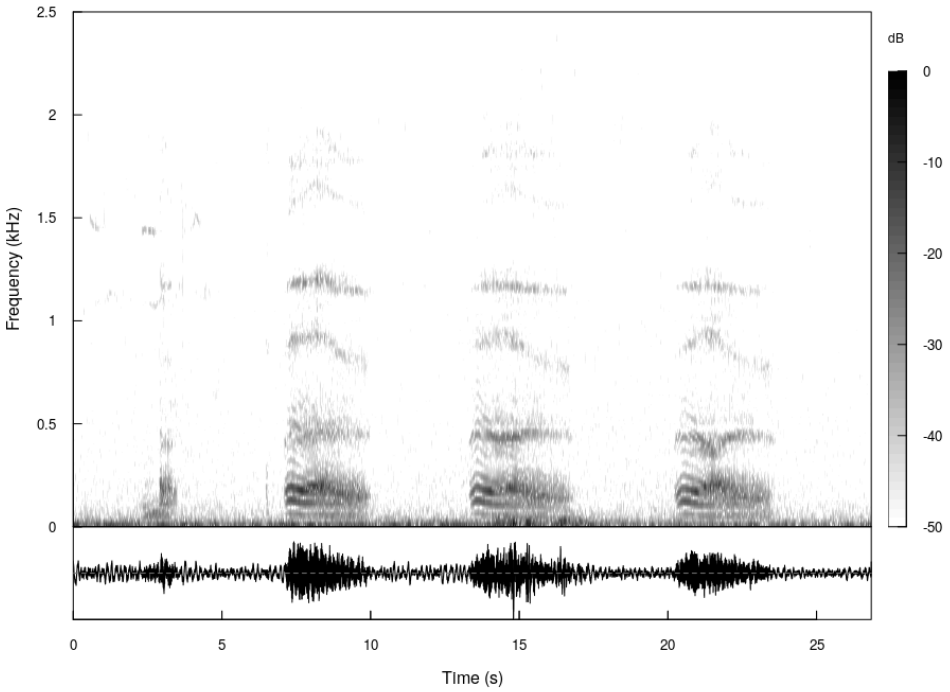

FIGURE 6.13. A sequence of *M. cataphractus* calls, composed of one short and three longer roars, most likely emitted by *M. cataphractus*, recorded on Hana River inside Taï National Park. Sampling rate 16 kHz, FFT size 1,024, Hanning window, overlap 93.75.

failed to detect their presence at rates comparable to the traditional spotlight survey methods. In the Bongo River region, only two calling events were identified as likely crocodile vocalisations: four drums, which most likely were produced by *O. tetraspis* (as described in Chapter 4), and two calls most likely produced by *M. leptorhynchus*. The social calls of adult crocodilians have a low dominant frequency, ranging between 20–250 Hz (Todd, 2007; Vergne et al., 2009), and often include infrasound (< 20 Hz) components (Dinets, 2013b). While many animals communicate at higher frequency range, some—most notably the forest elephants *Loxodonta cyclotis*—share the crocodilian acoustic space (Keen et al., 2017), and were present at both study sites (Chatelain et al., 2001; Lee et al., 2006). The lack of reference *M. leptorhynchus* call recordings, combined with the limited sample sizes of both the captive *M. cataphractus* and the suspected wild *M. leptorhynchus*, prevent definite conclusion that the two wild vocalisations belonged to *M. leptorhynchus*. However, the similarities of the call structure visualised on the spectrograms and the measured spectral properties of the two suspected *M. leptorhynchus* calls to the "long growl" recorded in captive *M. cataphractus*, were the basis for classifying these vocalisations as most likely emitted by crocodiles. In the south-western Taï National Park, only two calling events, comprising 14 calls in total, were identified as produced by crocodiles. The spectral properties of these calls were also similar to the "long growls" of captive *M. cataphractus*, and while the small sample size prevented

statistical comparisons, the sounds were different to those produced by forest elephants (Keen et al., 2017), suggesting positive identification as *M. cataphractus* calls.

Several factors may have contributed to the low success rate in crocodile detection using the passive acoustic monitoring. Crocodilians are most vocal during courtship and territory defence (Garrick and Lang, 1977; Vergne et al., 2009), and although *Mecistops* spp. (Shirley et al., 2018) and *O. tetraspis* (see Chapter 4) have been heard vocalising throughout the year, the peak in natural acoustic activity in the wild coincides with the onset of the rainy season and is likely related to breeding activity (Shirley et al., 2018). While the fieldwork in both Gabon and Côte d'Ivoire was planned to take place at the beginning of the rainy seasons in both countries, estimated to fall between November–December and April–May respectively (Waitkuwait, 1985; Lee et al., 2006), logistical issues with organisation delayed the field season in Gabon until January. Thus, while some vocal activity, as well as possible mating, could still have occurred there at the time of the study, it is likely that the peak courtship activity had finished before the commencement of the acoustic monitoring in the Bongo River region. Nevertheless, even though in Taï National Park the study coincided with the onset of the rainy season, the crocodile vocalisations were only recorded on two occasions, both in the same site. The mismatched timing of the acoustic monitoring was thus likely not the only reason for the lack of success in obtaining recordings.

The distance at which crocodilian calls can be heard is greater in the water than in the air, with the active space of *Alligator mississippiensis* bellows reaching 1.5 km in the water and 159 m in the air (Todd, 2007). At any given time during the study, recorders were placed in only two locations, limiting the monitored area where crocodiles could be detected, when compared to the range covered through a single spotlight survey (22.8 ± 9.3 km in the Bongo River region and 8.2 ± 1.4 km in south-western Taï National Park). Budget constraints prevented the use of a larger number of recording units in this project, but a larger network of recorders could increase the likelihood of detecting a call across the study site, as well as enable caller localisation (Wrege et al., 2017). The SM2+ recorders were connected to two hydrophones, with the stereo recordings providing opportunity for call localization by measuring the differences in amplitude and start time of the calls on the two channels (Blumstein et al., 2011; Frommolt and Tauchert, 2014). Unfortunately, all the vocalisations recorded in the wild were registered only with the aerial recorder, which due to software capabilities at the time of construction had one microphone only. Underwater sound detection can be affected by the depth at which the hydrophone is located, as well as the depth of the water body, with shallow water limiting sound detection (Desjonquéres et al., 2015; Browning et al., 2017). Freshwater habitats are also noisy, particularly those with fast-flowing water such as streams and rivers (Wysocki et al., 2007), due to the mechanical sounds produced by the water movement and objects coming into contact with the sensor, as well as the sounds emitted by other animals (Aiken, 1985; Giles et al., 2009; Knight and Ladich, 2014). This made manual call identification difficult, and the vocalisations recorded on the aerial recorders

could not be identified in the corresponding underwater recordings from the same location.

Manual call detection is time-consuming and labour-intensive, particularly when dealing with a large number of recordings. The call recognition is also prone to errors and depends on the skills and experience of the person performing the analysis (Heinicke et al., 2015). To mitigate this, automated and semi-automated call identification systems have been developed for a number of taxa (Blumstein et al., 2011; Browning et al., 2017; Gibb et al., 2019), however, many of those focus on higher-frequency calls, such as those of birds (Briggs et al., 2012), insects (Lehmann et al., 2014), primates (Heinicke et al., 2015), or bats (Rydell et al., 2017), which are easier to isolate from the background noise. The algorithms used for automated detection also require a sufficient number of the target species reference calls, which were not available for *Mecistops* at the time of this study. This, combined with the relatively high costs of the commercially available SM2+ recorders, made acoustic monitoring too labour intensive and too expensive when compared to the costs and time required to carry out standard spotlight surveys. However, recent developments in automated detection systems for the low-frequency elephant rumbles (Keen et al., 2017), combined with a larger number of cheaper open source acoustic recorders currently being developed (Browning et al., 2017; Whytock and Christie, 2017; Hill et al., 2018, 2019), could significantly reduce the costs and help in future adaptation of this method for automated crocodilian call identification in areas where traditional methods are more expensive. Although passive acoustic monitoring may not be a suitable method for *Mecistops* due to a potentially limited time window of high acoustic activity and the apparent low density of active individuals in both study sites, the system could be applied to surveys of the more terrestrial *Osteolaemus* spp., for which the traditional spotlight approach provided limited results (Shirley, 2010b). While only one *O. tetraspis* vocalisation bout was registered during the entire study period, the recorders in both Bongo River region and south-western Taï National Park were set primarily in the habitats preferred by *Mecistops* spp., where encounter rates with *Osteolaemus* were low. Vocalisations of *O. tetraspis* have been recorded through the passive acoustic monitoring system by the Elephant Listening Project inside the forests of Ivindo National Park in Gabon (Chapter 4), indicating potential use of this system for the forest-dwelling crocodilians, if situated optimally.

The playback surveys focused on *Mecistops*, and revealed a greater number of crocodiles than spotlight-only surveys, but this effect was larger in the Akaka region of Gabon than in the south-western Taï National Park. This may be a result of habitat differences between the two playback sites. Ngowe and Echira Rivers were surrounded by densely vegetated swamps and flooded areas (Matt Shirley, pers. comm.), which are a suitable habitat for *M. leptorhynchus* (Shirley et al., 2018), potentially hiding a number of crocodiles from the beam of the spotlight. Vegetation structure can conceal crocodiles and reduce detectability (Somaweera et al., 2018), with Ouboter (1996a) reporting lower number of *Caiman crocodilus* sightings in rivers with dense vegetation overhanging the banks. The Hana and Meno Rivers in Côte d'Ivoire were channelled and had relatively high banks, which both limited the aquatic habitat of *M. cataphractus* to the

river channel, and provided less vegetation to conceal the animals from the spotlight. The Akaka region provided more potential habitat for *M. leptorhynchus* adjacent to the survey transect than the rivers in south-western Taï National Park, which could explain the higher numbers of crocodiles detected through playback in Gabon. The wetlands in Akaka are situated near the eastern border of Loango National Park, with Ngowe River forming the Park border and Echira River flowing outside the Park, but through the protected area of the Gamba Complex (Fig. 6.1). While detection rates in the unprotected section of the river outside Taï National Park were lower, the overall mean detection rates during spotlight-only surveys were similar in both study sites (Akaka = 1.7 ± 0.5 km^{-1}; Taï National Park = 1.6 ± 0.8 km^{-1}). The protected status of the entire study area in Gabon (Lee et al., 2006), combined with relative remoteness from larger human settlements, likely lead to overall higher density of crocodiles in this study site when compared to Côte d'Ivoire, and provided the source of greater numbers of crocodiles that could be detected through the playback surveys.

Not all crocodilians encountered during spotlight and playback surveys were identified to species. The proportions of animals recorded as EO were in a similar range of 34–37% during the spotlight surveys in the two study sites and during the playback surveys in Taï National Park. While the data on species identification rate in the Akaka region was not available, Shirley et al. (2018) estimated approximately 46% of the crocodiles surveyed in Gabon between 2009–2010 were unidentifiable. This higher rate of EO individuals in Akaka, compared to other study sites, could be due to the presence of inaccessible wetlands adjacent to the survey routes (Shirley et al., 2018). The size class structures of *M. cataphractus* and *M. leptorhynchus* determined during the spotlight surveys were similar in the two study sites, with 89.6–95.2% of encountered animals falling into either juvenile or subadult categories. As reported from previous surveys (Shirley, 2010b), mature crocodiles were rarely sighted in both areas, which could be due to wariness of older individuals (Ron et al., 1998; Grigg and Kirshner, 2015), or low densities of breeding adults. Although the playback surveys attracted responses from both larger and smaller crocodiles (Table 5.7), incomplete data on size estimates, particularly sighted when travelling between the playback points, do not provide sufficient information on crocodilian size classes detected during the playback surveys. While the passive acoustic recording, which targeted adult crocodilians, did not provide sufficient information on their density and distribution, acoustic sensors could be incorporated into the playback survey protocols, particularly for *M. leptorhynchus* in densely-vegetated habitats, which appears to produce more vocal responses to call broadcasts (Shirley et al., 2018). The body-size dependent differences in acoustic parameters (Chapter 5; Chabert et al., 2015) could provide information of the body size of the responding animals.

While relying on spontaneous vocalisations proved to be impractical as a monitoring technique for *Mecistops*, playback survey methods that trigger visual or acoustic responses can increase detection rates in both *M. cataphractus* and *M. leptorhynchus*. This can provide basis for developing a standardised playback survey protocols for these species, and can be particularly

useful in areas with low densities of animals, or where the presence of *Mecistops* is suspected but not confirmed (Shirley et al., 2018). However, crocodilians can habituate to sounds quickly (pers. obs.; Nicolas Mathevon, pers. comm.), limiting the repeatability of this monitoring method. Varying the playback sequences that are broadcast during the survey may help mitigate this problem, but further research is still needed to determine the rate of habituation to distress call playback in *Mecistops* and its effect on detection rates. Therefore, similarly to monitoring mammals (Mills et al., 2001; Bryant et al., 2016), *Mecistops* playback surveys should not be repeated in the same area more than twice a year, until habituation to playback has been fully characterised. Additionally, while the surveys presented in this chapter were all conducted during the mating season, responses to hatchling and juvenile distress calls may differ between hatching season and times when young animals are less commonly encountered. Future studies examining the effect of season on the strength of response to distress calls could provide more guidance on the optimal timing for playback surveys.

Although not primarily targeted in this part of the study due to budget and time limitations, *Osteolaemus*, which prefer smaller streams and wetlands in the forest interior (Eaton, 2010) were not commonly encountered during spotlight and playback surveys. Monitoring techniques for this genus could benefit from a modified passive acoustic monitoring approach, incorporating a larger network of inexpensive, aerial acoustic sensors, and an automated vocalisation detection system.

CHAPTER 7

COURTSHIP AND UNDERWATER COMMUNICATION IN THE SUNDA GHARIAL (*Tomistoma schlegelii*)

Abstract

Adult crocodilians use acoustic communication primarily during courtship and territory defence. *Tomistoma schlegelii* is a member of the family Gavialidae, and inhabits densely vegetated peat swamps and flooded forests in Southeast Asia. The animals, particularly adults, are shy and difficult to observe in the wild and in captivity. As such, the species remains one of the least known crocodilians, with little information on adult ecology and behaviour to assist conservation efforts. To determine whether adult *T. schlegelii* are vocal during courtship, I used passive underwater acoustic monitoring to record 12 captive adult *T. schlegelii* kept in a semi-natural outdoor enclosure over a period of two months. Using hydrophone and video recordings, I also monitored a breeding captive pair of *T. schlegelii* housed indoors, in order to describe the behaviour and identify the acoustic signals produced during courtship. During the 18 successful *T. schlegelii* mating events recorded, the courtship behaviour followed that observed in other crocodilians, with the male initiating 93% of the interactions, all taking place in the water. However, acoustic signals were restricted to mating activity, and were only recorded in the indoor captive pair. During 24 vocalisation bouts recorded, *T. schlegelii* produced eight different acoustics signals: "croaks", single, double and triple "drums", as well as "rumbles", "moans", "bubbles" and "hisses". All croaks, rumbles and moans had a visible harmonic structure, but differed in duration and frequency of use. Croaks, which were short, low-frequency (89 ± 123 Hz) sounds, were the most common (66%) of the 216 acoustic signals recorded. Rumbles (164 ± 147 Hz) and moans (312 ± 119 Hz) were more rare (8% and 2% of calls respectively). Drums accounted for 17% of all signals, and were composed of short single or multiple low frequency (41 ± 9 Hz) pulses, with no visible harmonic structure. This is the first account of adult *T. schlegelii* vocalisations, suggesting the species uses short-range, underwater acoustic signals during courtship and mating, with little vocal activity outside of those events.

7.1 Introduction

Of the 28 currently recognised crocodilian species, courtship behaviour has been described in: three alligatorids, *Alligator mississippiensis* (Garrick and Lang, 1977; Vliet, 2000), *Alligator sinensis* (Thorbjarnarson and Wang, 2010) and *Caiman crocodilus* (Staton and Dixon, 1977); seven crocodylids, *Crocodylus acutus* (Garrick and Lang, 1977), *Crocodylus intermedius* (Thorbjarnarson and Hernández, 1993), *Crocodylus johnstoni* (Compton, 1981), *Crocodylus mindorensis* (Schneider et al., 2014), *Crocodylus niloticus* (Garrick and Lang, 1977), *Crocodylus rhombifer* (Augustine et al., 2017) and *Osteolaemus tetraspis* (Beck, 1978); and in one gavialid, *Gavialis gangeticus* (Whitaker and Basu, 1982). As such, courtship behaviour is yet to be described for more than half the recognised species, including six which are considered to be under the threat of extinction: *Crocodylus palustris*, *Crocodylus siamensis*, *Crocodylus suchus*, *Mecistops cataphractus*, *Mecistops leptorhynchus* and *Tomistoma schlegelii* (Shirley et al., 2018; IUCN, 2019). Information on social and mating behaviour could aid in conservation management and captive breeding programs (Schneider et al., 2014; Augustine et al., 2017), but this can be impossible to obtain in species that are difficult to observe in the wild.

In those species for which we do have information for regarding successful mating, males and females perform a sequence of behaviours, which forms courtship (Bradbury and Vehrencamp, 2011). In each of the species, the period of courtship usually lasts 6–8 weeks, with peak activity about one month before nesting (Garrick and Lang, 1977). This usually involves a series of visual, acoustic and olfactory signals (Bradbury and Vehrencamp, 2011) exchanged by the pair. Courtship and mating occur in the water and the behaviours can be classified into four categories generally happening in a sequence: (i) attraction and advertisement signals; (ii) initial pair formation; (iii) precopulatory behaviours; and (iv) copulation (Garrick and Lang, 1977; Augustine et al., 2017). While the behaviours serve different purposes between species and involve the use of different signals (Garrick and Lang, 1977; Augustine et al., 2017), general patterns and sequences are similar within the crocodylids and within alligatorids (Garrick and Lang, 1977; Thorbjarnarson and Wang, 2010).

Alligators (*A. mississippiensis* and *A. sinensis*) attract mates through loud bellowing displays, which often involve multiple individuals forming choruses (Garrick et al., 1978; Wang et al., 2007). In crocodylids (*Crocodylus* and *Osteolaemus*), advertisement behaviours can include vocalisations, bubble-blowing and headslaps (Garrick and Lang, 1977; Compton, 1981; Schneider et al., 2014; Augustine et al., 2017). Male gharials (*G. gangeticus*) produce infrasound and loud underwater popping signals with unique temporal patterns (Jailabdeen et al., 2018), that are not observed in other crocodilians.

After one of the animals approaches their partner, they engage in tactile interactions, which can last for several hours and include snout touching and rubbing (Vliet, 2000), vocalising, parallel swimming, pressing the partner underwater and mounting (Garrick and Lang, 1977; Vliet, 2000; Augustine et al., 2017). In the crocodylids, snout lifting by the female is commonly

observed at this stage (Compton, 1981; Thorbjarnarson and Hernández, 1993; Augustine et al., 2017), but this behaviour does not occur in alligators (Garrick and Lang, 1977; Vliet, 2000). Finally, copulation occurs when the male mounts the female and wraps his tail around and under her to bring the cloacas together (Vliet, 2000).

The differences between crocodilian families in the courtship vocalisations and behaviours could provide some guidance for the behavioural ecology of the species for which there is little information on mating behaviour. One exception is the Sunda gharial, *T. schlegelii*, which over the years has been classified as a member of the family Crocodylidae based on morphological interpretations (Brochu, 2003), while molecular evidence has placed it in the Gavialidae (Willis et al., 2007). Together with fossil data, a recent phylogenetic study (Lee and Yates, 2018) has reconciled these methods, and confirmed *Tomistoma* to be a gavialid together with *G. gangeticus*. The Gavialidae and Crocodylidae both belong to Longirostes, with Alligatoridae forming a sister taxon (Lee and Yates, 2018).

Very little is known about *T. schlegelii* communication, courtship and mating behaviour. Sunda gharials do not have a ghara–the bulbous narial growth at the tip of their snouts–which is a characteristic of the male *G. gangeticus* and is thought to be involved in sound production (Martin and Belleirs, 1977; Jailabdeen et al., 2018). Their cryptic colouration, combined with natural wariness have resulted in little information available on the basic ecology of adult *T. schlegelii* (Stuebing et al., 2006). Most information on the reproductive ecology of *T. schlegelii* comes from observations in captivity. The mating season is likely to vary geographically between captive and wild conditions. In Thailand, at Samutprakarn Crocodile Farm, Trutnau and Sommerlad (2006) witnessed mating in October 1985. At Jong's Crocodile Farm in Sarawak, *T. schlegelii* mating has been observed between March–May (Johnson Jong, pers. comm.). Courtship and mating in East Kalimantan likely occurs between March and June (Staniewicz et al., 2018).

Although *T. schlegelii* have been kept in zoological collections around the world for decades (Fernandez-Hoyo and Recuero, 2009), until recently there has been little success in breeding these animals in captivity outside of Southeast Asia (Trutnau and Sommerlad, 2006). In 2016–2018, successful breeding occurred in several North American Zoos, including San Antonio Zoo, Zoo Miami and Audubon Zoo, as well as the first hatching of *T. schlegelii* in the UK, at the Crocodiles of the World Zoo (Litton et al., 2018).

Here, I provide the first description of the courtship behaviour in *T. schlegelii* using behavioural observations from their first successful mating in the UK. I also present the acoustic signals associated with courtship and mating, which represent the first detailed description of adult *T. schlegelii* vocal communication.

7.2 Methods

In this study, I recorded a mixed sex group of 12 adult *T. schlegelii* at Jong's Crocodile Farm in Sarawak, Malaysia, and two adult *T. schlegelii*, a male and a female, held at Crocodiles of the World Zoo in Oxfordshire, UK. These UK animals were raised at Jong's Crocodile Farm and moved into their current exhibit in July 2016.

7.2.1 Behavioural observations

7.2.1.1 Jong's Crocodile Farm

The *Tomistoma* enclosure is situated in a woodland at the southeast corner of the farm and is divided into a deep water area (approx. 100 × 30 m), consisting of a long lake (approx. 3 m at deepest point) with forested banks, and the land area (approx. 60 × 25 m) with three 7 × 4 m pools surrounded by a shaded basking area that becomes partially flooded after heavy rains. Due to the large area of the enclosure and few accessible viewing points, observations of *T. schlegelii* behaviour were carried out *ad libitum*. Between 26 April and 5 July 2016 I observed the crocodiles in daytime during the opening hours of the Jong's Crocodile Farm (0900–1700 hours) for 0.5–2 hours per day over 26 days (28 hours in total).

7.2.1.2 Crocodiles of the World

The crocodiles were housed in a 15 × 12 m indoor enclosure containing a pool and a land basking area. The pool measured 2 m at its deepest point, with a shallow step area 60–70 cm deep. The average water temperature in the pool was 29°C and the average air temperature in the enclosure was 32°C. The enclosure was fitted with a CCTV camera with the view of the basking area and the pool, recording video at a rate of one frame/s. I identified the behaviour of the two *T. schlegelii* recorded on 6 h and 18 min of video from 17 days (30 December 2016 to 19 February 2017) using the nomenclature developed for *A. mississippiensis* (Garrick and Lang, 1977; Vliet, 1987, 2000). Male and female were recognised by their body size. Using the time stamps on video and audio recordings, I matched the behaviour of eight mating events to the vocalisation bouts on acoustic recordings.

I classified the behaviours based on the ethogram created for *A. mississippiensis* by Vliet (2000). Where available, I supplemented my records with anecdotal accounts of *T. schlegelii* courtship observations from the grey literature.

7.2.2 Acoustic recordings

7.2.2.1 Jong's Crocodile Farm

I installed two Wildlife Acoustics Song Meter 2+ recorders, each connected to two HTI-96-MIN hydrophones in the water in the crocodile enclosure. Initially the units were placed 20 m away

from each other in the river area of the enclosure and on 12 May one of the units was moved to the land area, with the hydrophones installed in the middle pool. I placed each hydrophone inside a 3 m long, 1.5 cm diameter PVC pipe, with the pipes in each unit 4 m away from each other. Water and PVC have similar sound transmission properties, thus allowing the acoustic signal to reach the hydrophone without exposing the equipment to the animals. Nevertheless, the presence of the PVC pipe may have affected the underwater signals recorded. The crocodiles were recorded continuously for 58 min every hour at 4 kHz sampling rate, from 26 April to 5 July 2016 (a total of 1,680 hours over 70 days). This corresponded to the predicted breeding season in Borneo.

7.2.2.2 Crocodiles of the World

Mating behaviour was first observed by the zoo staff in December 2016. I installed a 2.5 m long, 1.5 cm diameter PVC pipe along the wall of the enclosure and reaching into the water of the pool. This acted as a protective case for the HTI-96-MIN hydrophone, which was lowered into the water. Using a Wildlife Acoustics Song Meter 2+ recorder, I recorded the animals continuously for 58 min every hour at 4 kHz sampling rate, between 14 January–24 February 2017 (a total of 847 hours over 39 days).

7.2.3 Call analysis

I manually identified the *T. schlegelii* vocalisations on spectrograms using SASLAB PRO 5.2.12 (Avisoft Bioacoustics, 2017) and measured the call duration. If a call was composed of several elements (where the time differences between each element was < 0.5 s), I also measured the number of pulses, pulse duration and the inter-pulse interval. The measurements of central peak frequency, fundamental frequency and bandwidth were taken automatically using the SASLAB PRO automated call parameter measurement feature. Statistical analysis was performed using R 3.6.0 statistical software (R Core Team, 2018).

7.3 Results

7.3.1 Courtship behaviour in adult *Tomistoma schlegelii*

No mating was observed at Jong's Crocodile Farm between 26 April and 5 July 2016. On 26 April, one of the male *T. schlegelii* produced a head slap, followed by narial geysering (Table 7.1) when close to a smaller individual, but this behaviour was not registered on the acoustic recorder. Two *T. schlegelii* females built nests: one around 20 April, and the other on 16 June, suggesting that courtship and mating had occurred before and during the monitoring period, but no vocalisations were recorded.

TABLE 7.1. The behaviours observed during courtship of *T. schlegelii* recorded at Crocodiles of the World, UK (CotW) and Jong's Crocodile Farm, Malaysia (JCF). Additional anecdotal accounts of these behaviours from other breeding facilities are marked with an asterisk and refer to sightings at Bronx Zoo, USA (Kevin Torregrosa, pers. comm.), Samutprakarn Crocodile Farm, Thailand (SCF) (Trutnau and Sommerlad, 2006), and crocodile farms in Jambi Province (JPF), and Sumatera Utara Province (SUF) Indonesia (Bezuijen et al., 1997). Notation *n* refers to the number of times the behaviours were recorded on video at CotW.

Behaviour	**Description**	**Site**	***n***
Head slap	Head is raised with the jaws open, head is then rapidly slapped down on the water surface	CotW, SCF*	1
SAV	Production of sub-audible vibrations (infrasound)	CotW	
Swim around	One animal (usually male) swims around and/or circles the other (usually female)	CotW, SUF*	1
Head lift	Head is lifted out of the water with the jaws open	CotW, SUF*	2
Approach	One animal approached the other in the water until they make physical contact	CotW, JCF, BZ*, JPF*, SUF*	15
Snout rubbing	Male and female rub their jaws against each other	CotW, BZ*	13
Vocalising	Production of vocalisations	CotW, BZ*	
Bubbles	Large air exhalation underwater, often associated with submerging	CotW, BZ*	
Narial geysering	Rapid release of air from the external nares, releasing up a stream of water	JCF, BZ*	
Mounting	One animal dorsally mounts another	CotW, JPF*, SUF*	18
Tail under	Top animal wraps the tail around and under the bottom animal	CotW, JPF*, SUF*	17
Roll	When mounted, the top animal rolls in order to tail search	CotW	11

There were 24 *T. schlegelii* vocalisation bouts recorded between 15 January and 24 February 2017 at Crocodiles of the World. The bouts lasted between 4–55 min, with the mean bout duration of 20 ± 15 min. Ten of the bouts have corresponding video footage, showing courtship and mating; videos for the remaining 14 bouts were not available. There were a further eight mating events recorded on camera with no corresponding audio; three were recorded before the acoustic recorder was deployed (30 December 2016 to 13 January 2017), and five were not detected on the acoustic recorder. The majority of activity took place when the zoo was closed to visitors, with 59% of the observed mating events and vocalisation bouts occurring between 1600–1800 hours (Fig. 7.1).

During courtship, *T. schlegelii* displayed 12 behaviours classified in Table 7.1. Generally, after approach, which was initiated by the male in 93% of the events observed, the animals rubbed their heads and jaws against each other, and the male pushed the female underwater and mounted her. The mounting lasted between 1–36 min, with the mean duration of 16 min. The male was observed wrapping his tail around and under the female in 94%, and rolled in 61% of the mating events (Table 7.1). The pair stayed together 2–55 min (mean = 19 ± 17 min), after which they separated. Both animals vocalised during courtship and mating.

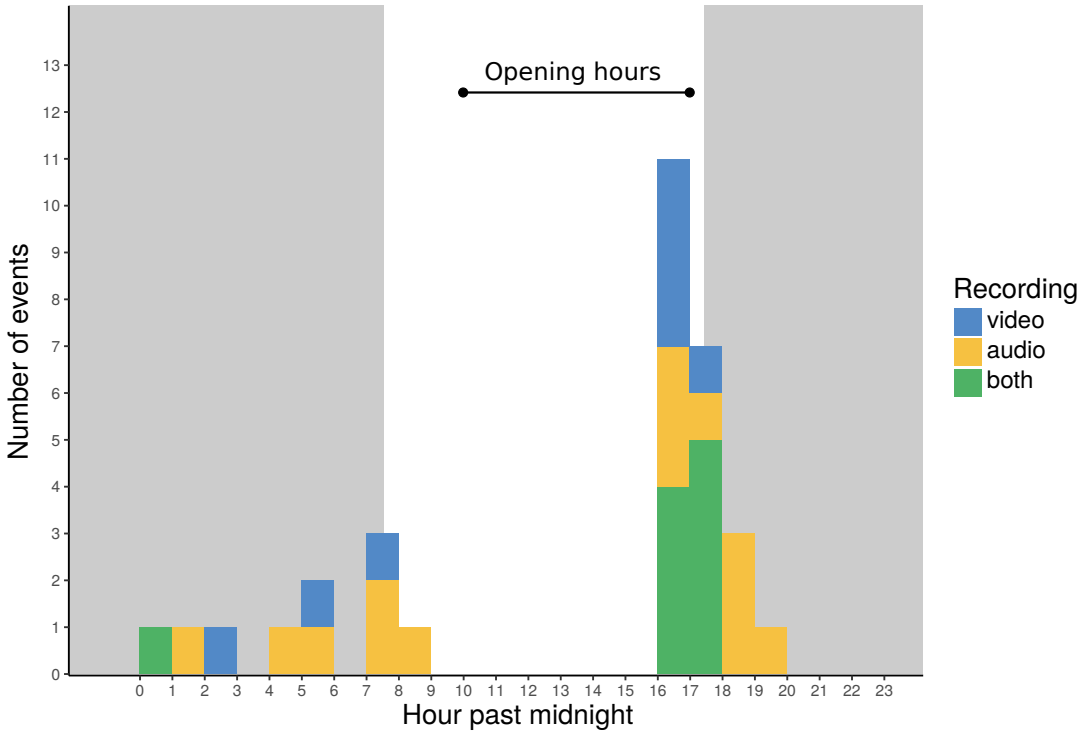

FIGURE 7.1. The distribution of the 24 vocalisation bouts over the 24 h period. The 10 bouts that were confirmed as mating events on video are marked in green. Additional 14 vocalisation bouts not recorded on video are marked in yellow. Further eight mating events which occurred between 30 December 2016 and 6 February 2017 and were not registered on the acoustic recorder but on video only, are marked in blue. The bins include all events during the hour. White background represents daylight, and grey background represents night. The zoo opening hours (1000–1700) are marked with a line.

7.3.2 Call types and call parameters

Tomistoma schlegelii produced eight different acoustic signals during courtship, identified here as single, double and triple "drums", "croaks", "rumbles", "moans", "bubbles" and "hisses" (Fig. 7.2).

The most common sound produced by *T. schlegelii* was the croak, accounting for 65.6% of all sounds (Table 7.2). The croaks were composed of more than three pulses, with the interval between the pulses shorter than 0.07 s. They were short (mean duration = 0.31 ± 0.08 s) and had a visible harmonic structure, with mean fundamental frequency 26 ± 12 Hz.

Drums were short, (mean duration = 0.24 ± 0.19 s), low frequency (41 ± 9 Hz) pulses with no visible harmonic structure. Single drums were the most common type of drum, and accounted for 10.7% of all sounds recorded (Table 7.2). Double and triple drums were less common, accounting for 4.7% and 1.8% of all sounds respectively.

Rumbles were longer than croaks (mean duration = 1.78 ± 0.48 s), low frequency sounds

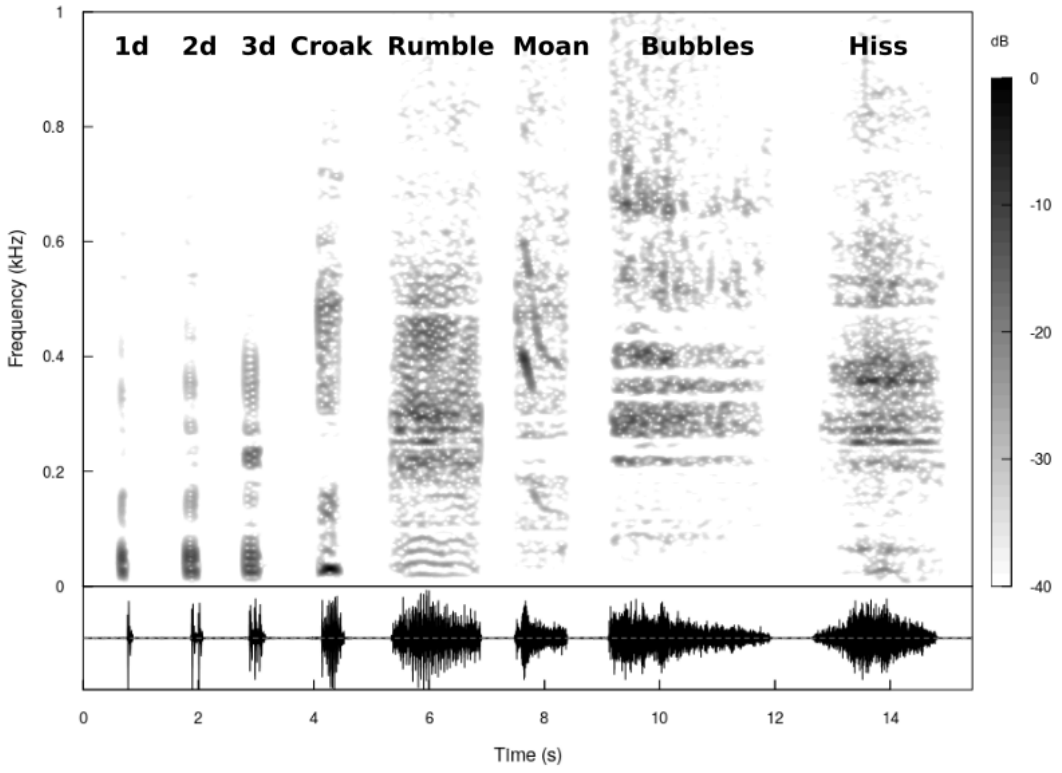

FIGURE 7.2. Composite spectrogram with examples of the six calls produced by adult *T. schlegelii* during mating: single drum (1d), double drum (2d), triple drum (3d), croak, rumble and moan, as wells as the two other sounds recorded that are associated with mating behaviour: bubbles and hisses. Sampling rate 4 kHz, FFT size 1,024, Hanning window, overlap 93.75.

with visible harmonic structure. The mean dominant frequency was 164 ± 147 Hz, with very low fundamental frequency (18 ± 10 Hz). Rumbles accounted for 8.4% of all sounds recorded (Table 7.2).

Moans had multiple, downsweeping harmonics, with higher mean dominant frequency 312 ± 119 Hz and mean fundamental frequency 141 ± 35 Hz. They were rare, accounting for 2.3% of all sounds recorded.

Bubbles and hisses were longer, with more energy in the higher range of the frequency spectrum and no visible harmonic structures (Table 7.2). Both of these sounds were rare (bubbles = 3.7% of all sounds; hisses = 2.8%), and in case of hisses were suspected but not confirmed to be produced by *T. schlegelii*. As bubbles are respiratory sounds produced during exhalation underwater, together with the hisses they were excluded from further analysis of acoustic parameters.

To evaluate the differences between the *T. schlegelii* acoustic signal types, I used a principal component analysis (PCA) (Fig. 7.3). The peak frequency of the call (case loading = 0.630),

TABLE 7.2. Acoustic characteristics (mean ± SD) of the *T. schlegelii* call types recorded underwater. Values of the dominant (max.) frequency, fundamental frequency (pitch) and bandwidth were measured at the centre of the call.

Call type	***n***	**Duration (s)**	**Interval (s)**	**Max. frequency (Hz)**	**Pitch (Hz)**	**Bandwidth (Hz)**
1 Drum	23	0.10 ± 0.01		41 ± 8		117 ± 33
2 Drums	10	0.44 ± 0.03	0.17 ± 0.01	45 ± 8		83 ± 14
3 Drums	4	0.58 ± 0.11	0.14 ± 0.02	36 ± 12		81 ± 17
Croak	141	0.31 ± 0.08		89 ± 123	26 ± 12	512 ± 190
Rumble	18	1.78 ± 0.48		164 ± 147	18 ± 10	523 ± 168
Moan	5	0.63 ± 0.14		312 ± 119	141 ± 35	306 ± 92
Bubbles	8	2.06 ± 1.54		407 ± 154		$1,068 \pm 562$
Hiss	6	1.32 ± 0.35		299 ± 79		$1,192 \pm 326$

combined with bandwidth (0.562) and call duration (0.536) explained 46.7% of variance (PC1). Call duration (case loading = −0.757) and bandwidth (0.650) had the strongest effect on PC2, which explained 28.8% of the variance.

I carried out a second PCA to evaluate the effect of fundamental frequency on the separation of the vocalisations which had visible harmonic structures: croaks, moans and rumbles (Fig. 7.4). The first component (PC1) accounting for 31.1% of the variance was primarily influenced by the peak frequency (case loading = −0.713), call duration (−0.549) and bandwidth (−0.434). The fundamental frequency (case loading = −0.840) associated with PC2 accounted for 28.6% of the variance.

During four of the vocalisation bouts, there were 1–2 sequences comprised of 4–10 croaks, 1–2 triple drums and a moan (Fig. 7.5). These sequences were 6.9 ± 1.5 s long and calls had overlapping elements, suggesting both animals were involved in call production, forming a duet.

7.4 Discussion

Tomistoma schlegelii show complex behavioural patterns during courtship, employing visual, tactile and auditory cues. Although the animals produce a range of acoustic signals, these appear to be mostly short, underwater, low-frequency sounds used primarily in short-range communication before and during the mating events. As such, *T. schlegelii* remains an unusually quiet crocodilian species, providing further evidence for a closer phylogenetic affinity to gavialids rather than Crocodylidae.

Crocodilian behaviour is conserved within and between species (Brazaitis and Watanabe, 2011), with many of the courtship behaviours, including circling, head lift, head slap, bubbling, snout rubbing and narial geysering considered to be ancestral traits of all crocodilians (Setner, 2008). These behaviours were also seen in the *T. schlegelii* at both study sites and have been observed at other breeding facilities (Bezuijen et al., 1997; Trutnau and Sommerlad, 2006)

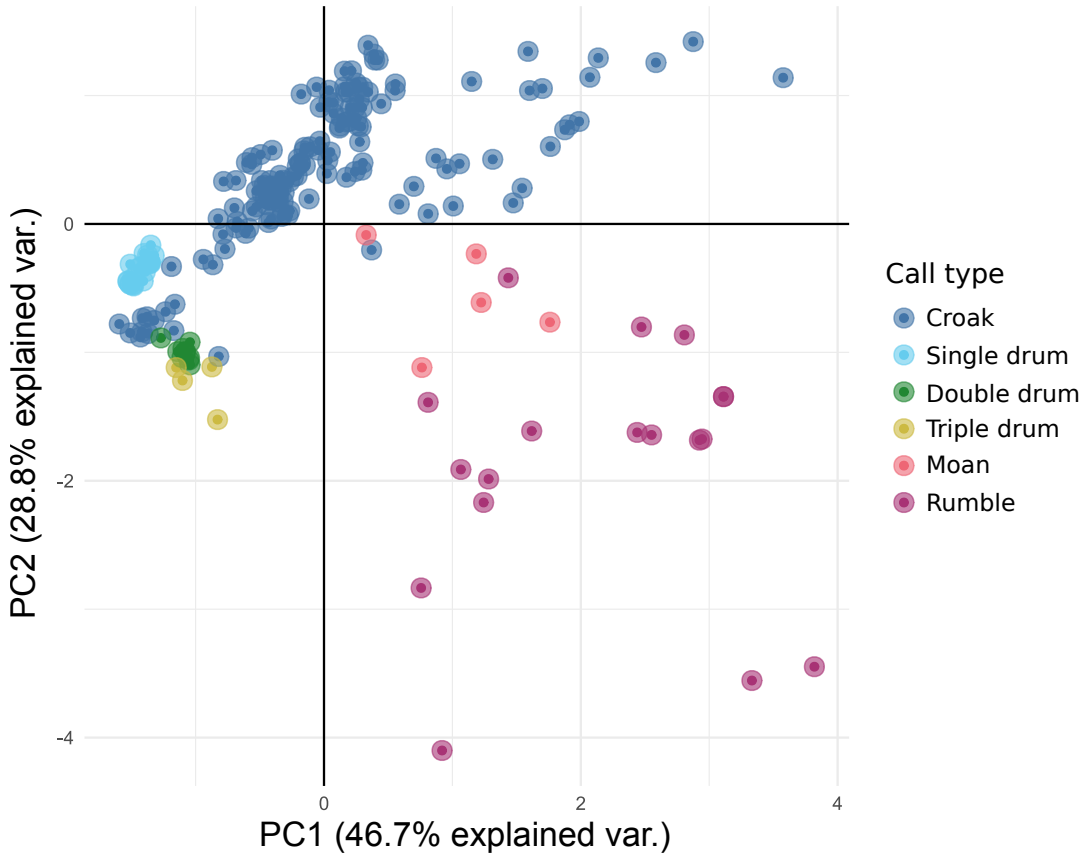

FIGURE 7.3. PCA results showing the division of *T. schlegelii* calls in the acoustic space. Distribution along the PC1 is primarily based on peak frequency (case loading = 0.630), and PC2 is based on call duration (−0.757) and bandwidth (0.650). Bubbles and hisses have been removed.

(Kevin Torregrosa, pers. comm.). The male initiated the majority of mating events recorded by approaching the female, and tactile interactions such as snout rubbing and pressing the female underwater generally preceded mounting and copulation. A broadly similar pattern has been observed in other crocodilians (Garrick and Lang, 1977; Thorbjarnarson and Wang, 2010; Augustine et al., 2017). The duration of these courtship behaviours in *T. schlegelii* was also similar to those of *Alligator* and *Crocodylus*, lasting from a few minutes up to one hour (Garrick and Lang, 1977).

While 11 of the 12 courtship behaviours reported here were observed at Crocodiles of the World, the narial geysering was only noted at Jong's Crocodile Farm (Table 7.1). This could be a result of the video equipment recording one frame per second, leading to certain rapid actions being missed. The videos also did not comprehensively cover the complete duration of the mating season, thus some rarer *T. schlegelii* behaviours occurring only during undocumented mating events might not have been recorded. Olfactory cues were also not detectable using the

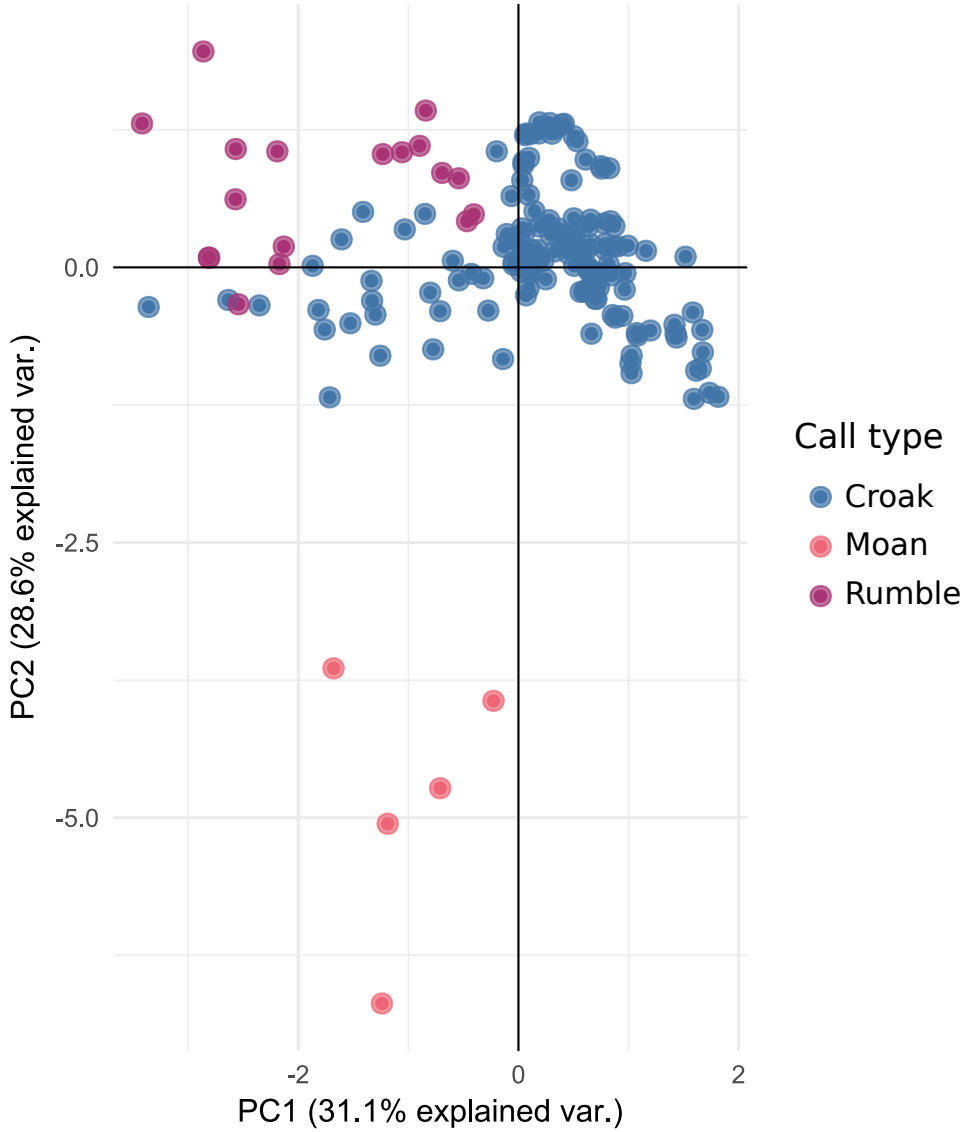

FIGURE 7.4. PCA results showing the division of *T. schlegelii* vocalisations in the acoustic space. Distribution along the PC1 is primarily based on peak frequency (case loading = −0.713), call duration (−0.549) and bandwidth (−0.434), and PC2 is based on the fundamental frequency (−0.840).

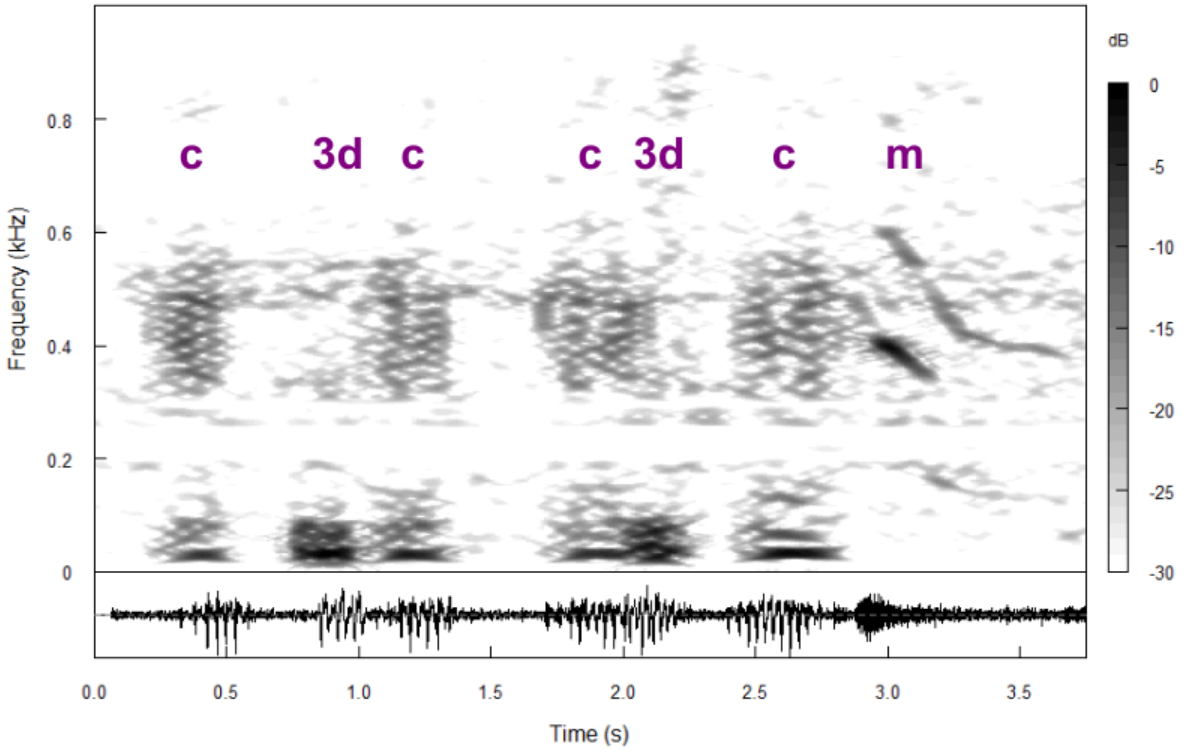

FIGURE 7.5. A sequence of calls composed of croaks (c), triple drums (3d), and a moan (m), produced by the *T. schlegelii* pair during mating. Sampling rate 2 kHz, FFT size 512, flat top window, overlap 93.75.

monitoring techniques applied here but are likely produced by *T. schlegelii* and "strong odour" has been reported by one of the crocodile farmers in Indonesia (Bezuijen et al., 1997). Olfactory stimuli are used in courtship and combat displays, and Vliet (1987) reported observing "oily sheen" on the water surface near *A. mississippiensis*. The function of the odour, which likely originates near the cloaca (Vliet, 1987), is not known.

Vocalisations, including infrasound (SAV) and bubble blowing were performed by captive *T. schlegelii* at Crocodiles of the World, and formed part of the courtship. While the animals did not produce loud roars or bellows associated with the courtship of *Alligator* and *Crocodylus* (Garrick and Lang, 1977), the underwater recordings revealed a range of acoustic signals previously unreported in *T. schlegelii*.

Croaks were the most common of the sounds emitted and they appear similar to coughs (or "chumpfs") described by Garrick et al. (1978) in *A. mississippiensis*. Both coughs and croaks had similar peak frequencies (croaks = 89 Hz; coughs = 75 Hz) and duration (croaks = 0.31 s; coughs = 0.29 s) and were used during courtship at short range (Garrick et al., 1978). Vliet (1987) also reported soft, low frequency (< 50 Hz) vocalisations called "flutter", which were produced

by *A. mississippiensis* during pair formation and when making tactile contact. The flutter had no visible harmonic structure (Vliet, 1987) and could refer to the coughs reported by Garrick et al. (1978), though as Vliet (2000) noted, these sounds were not cough-like. Similar short-range vocalisations were produced by *A. sinensis*, which emitted "toots" (Wang et al., 2007), "chuffs" and "burps" (Thorbjarnarson and Wang, 2010).

The PCA revealed differences between the drums, croaks and rumbles: drums were generally shorter and had a lower peak frequency than croaks, while rumbles were longer, with a higher peak frequency. Although categorised as discrete call types, this apparent diversity could also reflect continuous variation in *T. schlegelii* calls. Both drums and rumbles were less common than croaks, but their function remains unknown. The moans were only produced as part of the call sequences, following croaks and drums. As with drums and rumbles, playback experiments might reveal the function of these calls and the possible presence of syntax in *T. schlegelii* courtship vocalisations.

Different authors have used a variety of names for the short-range vocalisations of *Alligator* spp., including flutters, coughs, chumpfs, toots, moos and whines (Garrick et al., 1978; Vliet, 1987; Wang et al., 2007). While some of theses names could be synonyms referring to the same sound, the presence of drums, croaks and rumbles produced by *T. schlegelii* suggests that a range of several different low-frequency sounds are emitted during crocodilian courtship. As courtship and mating occur primarily in the water (Trutnau and Sommerlad, 2006), which complicates recordings, it is possible that other species also produce a wider range of signals than previously documented. Most of the studies of crocodilian courtship to date have not used hydrophones (Garrick and Lang, 1977; Vliet, 1987; Wang et al., 2007; Schneider et al., 2014; Augustine et al., 2017) and the recent underwater recordings of *G. gangeticus* revealed the presence of underwater sounds produced by adult males, which were previously thought to be jaw slaps (Jailabdeen et al., 2018). Thus, both members of the family Gavialidae produce SAVs and underwater sounds during courtship, but none of the loud bellows or roars used by other crocodilians.

The sounds produced by *T. schlegelii* differ from the popping sounds of *G. gangeticus* in both acoustic properties and context. Male gharials produce underwater pops in response to disturbance, territory patrolling, male-male contests and courtship (Jailabdeen et al., 2018), while *T. schlegelii* appear unusual amongst crocodilians, being vocal only during courtship and mating. Although the presence of just one pair of animals at Crocodiles of the World rules out acoustic male-male interactions and likely eliminates the need for patrolling behaviour, there were also no acoustic signals recorded at Jong's Crocodile Farm, which housed a larger mixed-sex group of individuals. A study of animal behaviour in captivity has significant limitations: a small number of individuals who are familiar with each other, share the same pool and are often in each other's line of sight. These conditions, very different to those found in flooded forests, could have prompted *T. schlegelii* to use visual and olfactory cues more, and removed the need for advertising their location or territory vocally. Although crocodilians use different

communication signals in continuous and fragmented habitats (Dinets, 2011), the individual animals do not change their signals in response to habitat changes (Dinets, 2013a). Crocodilian acoustic repertoires are conserved within the species in captivity and in the wild (Vergne et al., 2009), and the evidence of other species vocalising in the same facility (Sean Foggett, pers. comm.) suggest that *T. schlegelii* behaviour documented here is likely typical for the species. The animals produce a number of acoustic signals during short-range communication, which are associated with courtship and could be detected at close range in an indoor enclosure, but not in semi-natural outdoor conditions at Jong's Crocodile Farm. Based on personal communication with A. Karlon and U. Youngprapakorn, Dinets (2013b) stated that while *T. schlegelii* produce infrasound, head slaps and assume the HOTA (head-oblique, tail-arched) posture, they do not produce vocal sounds unless physically provoked, further supporting the findings that they are not vocal outside the courtship and copulation context.

Unlike other crocodilians, which mate primarily in the mornings (Garrick et al., 1978; Compton, 1981; Kofron, 1991; Vliet, 2000; Schneider et al., 2014), *T. schlegelii* courtship and mating at Crocodiles of the World occurred mostly at dusk and at night. Similar mating activity pattern was reported from *T. schlegelii* breeding in Zoo Negara in Malaysia (Mathew et al., 2011), and as very little activity was observed during the day at Jong's Crocodile Farm, it is likely the animals there were also nocturnal. *Tomistoma* are shy and sensitive to human observers (Johnson Jong, pers. comm.), thus the timing of their courtship and mating matching the closing times of the zoo indicate that the presence of visitors could also inhibit mating attempts. Although previous activity monitoring of the *T. schlegelii* at Crocodiles of the World suggests that the species may be primarily nocturnal (unpublished data), lack of behavioural field observations prohibit definite conclusions on daily activity patterns.

Courtship in *T. schlegelii* appears similar to behaviours displayed by other crocodilians, though unlike the *Alligator* and many *Crocodylus*, it does not involve loud advertisement roars or bellows. Together with the presence of underwater acoustic signals, which are common for both gavialids, it corroborates the phylogeny of ancestral crocodilian courtship behaviours derived by Setner (2008), suggesting that loud vocal sounds were likely lost in Gavialidae. The differences in underwater signals used by *T. schlegelii* and *G. gangeticus* could be related to morphological differences (the presence or absence of ghara), or the different habitats used (Dinets, 2013b). Both species are found primarily in continuous aquatic habitat (Dinets, 2013b), yet *G. gangeticus* prefers large streams and rivers with sand, grassy or rocky shores (Trutnau and Sommerlad, 2006), while *T. schlegelii* is more common in densely vegetated peat swamp forests and lowland forest rivers (Bezuijen et al., 1997; Staniewicz et al., 2018), where the lower-frequency calls will attenuate less (Wang et al., 2007).

Although the behaviour of shy, nocturnal, aquatic animals is difficult to observe in both captive and wild conditions, future acoustic and high frame-rate video monitoring of a larger group of captive *T. schlegelii* could help determine the context of individual call types and the call

sequences, as well as the identity of signals used in other social interactions outside of courtship. Higher acoustic recording sampling rates could also provide information on possible higher frequency vocalisations not recorded in this study. *Tomistoma schlegelii* is rarely kept in captivity, with only small numbers of adults kept outside southeast Asia (Trutnau and Sommerlad, 2006; Fernandez-Hoyo and Recuero, 2009). Thus, still little information is available on the species' social behaviour outside of courtship and mating, and the effect of larger number of animals on the breeding success in captivity. Observations on *G. gangeticus* also revealed individual signatures in the temporal patterns of the underwater pops (Jailabdeen et al., 2018), while the formant frequencies of an adult *Alligator* bellow provide information on the body size of the crocodilian (Reber et al., 2017). Further analysis of calls of a larger number of *T. schlegelii* could identify if any of the call properties encode an individual's signature, which could be used to identify animals during the acoustic monitoring.

The results presented here indicate that *T. schlegelii* uses short-range acoustic signals during courtship and mating, with little vocal activity outside of those events. As such, unlike other crocodilians, *Tomistoma* may not be the best candidate for the use of acoustic methods in monitoring wild populations. Nevertheless, this chapter provides a basis for further research on the social behaviour and captive breeding of this threatened species, as well as for investigation into the diversity of underwater signals during crocodilian courtship.

CHAPTER 8

GENERAL DISCUSSION

8.1 Acoustic communication in rare crocodilians

Adult *Mecistops*, *Osteolaemus* and *Tomistoma* all produce a diversity of acoustic signals akin to that previously reported only in *Alligator sinensis* (Thorbjarnarson and Wang, 2010). Further research is still required in order to describe and catalogue the vocal repertoire of adult *Mecistops* spp., as well as *Osteolaemus osborni* and *Osteolaemus* aff. *tetraspis*. While genetic and, to a small extent, morphological differences were the basis for recognition of cryptic diversity in both of these African genera (Eaton et al., 2009; Shirley et al., 2015, 2018), it is currently unknown whether there are differences in behaviour, or adult communication as well. Acoustic divergence in cryptic species living in sympatry can lead to reproductive isolation and in consequence to speciation (Kingston et al., 2001; Braune et al., 2008). However, as the species within *Mecistops* and within *Osteolaemus* are allopatric (Shirley et al., 2015; Smolensky, 2015), there is little evolutionary pressure for acoustic divergence in adult communication associated with courtship and mate choice. Therefore large differences in acoustic repertoire between *M. cataphractus* and *M. leptorhynchus*, as well as between the three *Osteolaemus* spp. would not be expected except for genetic drift. Nevertheless, information on acoustic repertoire for all African species could determine whether niche segregation between the sympatric *Crocodylus*, *Mecistops* and *Osteolaemus* described in Chapter 3 extends to acoustic separation, and provide a baseline for future species identification from acoustic recordings.

The diversity of acoustic signals presented here could indicate the presence of similarly diverse vocal repertoires in other crocodilians, particularly the species inhabiting densely vegetated and forested environments. For example, South American dwarf caimans, *Paleosuchus palpebrosus* and *Paleosuchus trigonatus*, are diminutive species inhabiting small, fast-flowing streams and

rivers in the Amazon rainforest (Trutnau and Sommerlad, 2006). While there are currently no published records of adult *Paleosuchus* spp. vocalisations, Dinets (2013b) reported anecdotal evidence that they produce short, bark-like roars, as well as infrasound. As their ecology is analogous to that of *Osteolaemus*, spending a large proportion of their time on the forest floor away from larger water bodies (Magnusson and Lima, 1991), it is possible that they could also produce a similar range of acoustic signals for intraspecific communication.

However, ecological similarities may not translate into the same use of acoustic signals between the different crocodilian genera and families. Although *Mecistops* spp. and *T. schlegelii* have similar morphology, ecology and habitat preferences (Bezuijen et al., 2014; Shirley et al., 2018), these similarities are analogous, as the former is a member of Crocodylidae and the latter, Gavialidae (Lee and Yates, 2018). The vocal behaviour of the two is very different, with *T. schlegelii* producing little sound outside of mating and copulation, while adult vocalizations of *Mecistops* spp. are frequently heard throughout their range (Shirley, 2010a; Shirley et al., 2018). The phylogenetic distance between *T. schlegelii* and the crocodylids (Lee and Yates, 2018) could account for the differences in communication behaviour. Setner (2008) identified homologous crocodilian behaviours by mapping communication traits onto a phylogeny of seven species (six *Crocodylus* spp. and *Alligator mississippiensis*). While only two genera were included in that analysis, the information presented in this thesis, together with studies on *A. sinensis* (Wang et al., 2007; Thorbjarnarson and Wang, 2010), *Gavialis gangeticus* (Jailabdeen et al., 2018), as well as possible future studies on communication behaviour in the caimans (*Caiman*, *Melanosuchus* and *Paleosuchus* spp.), could allow for detailed analysis of the phylogenetic distribution of behavioural characteristics in all crocodilians.

While all the species presented in this thesis produced a range of different call types, further research is still needed to determine their meaning and context. As all species studied here are rare, both in the wild and in captivity (Fernandez-Hoyo and Recuero, 2009; Schmidt, 2015; Shirley et al., 2018), limited availability of individuals and the difficulties in obtaining sufficient numbers of naïve animals for playback experiments currently remains a major obstacle.

Additionally, both *Osteolaemus* spp. and *T. schlegelii* produced several specific sequences of different call types emitted in particular orders. The ability to combine individual vocal elements into sequences has been described in birds and mammals (Collier et al., 2014), but not in reptiles. Although the ability to create new, more complex meanings by combining simple elements (syntax) has previously been considered unique to human language (Collier et al., 2014), experimental evidence from bird calls has shown that it may have evolved independently in other animals (Suzuki et al., 2016). While further studies are needed to determine the meanings of individual call sequences, their presence in *Osteolaemus* and *T. schlegelii* acoustic communication could lead to discovery of a first example of syntax in reptiles. Furthermore, as crocodilians, together with birds, are modern representatives of archosaurs (Brazaitis and Watanabe, 2011; Grigg and Kirshner, 2015), confirming the presence of syntax in both groups could suggest it is a feature

that could be common to all archosaurs, including the extinct dinosaurs and pterosaurs.

8.2 New methods for monitoring crocodilians

Crocodilians living in forested habitats vary in ecology and behaviour, resulting in no single monitoring method being best for all three genera tested. The detectability rates during spotlight-only surveys can be skewed by niche partitioning between sympatric crocodilians, especially when survey efforts are not equal between niches (see Chapter 3), and the crocodiles that are submerged at the time of survey or are in areas not accessible to the survey vessel are undetected (Bayliss, 1987; Grigg and Kirshner, 2015). Although methods such as mark-recapture can be used to estimate the true population size and thus assess the percentage of population detectability during spotlight surveys (Bayliss, 1987), crocodilian capture is labour-intensive, time-consuming, and often difficult and dangerous, making mark-recapture unsuitable for rapid assessment and short-term monitoring projects. Despite their drawbacks, spotlight surveys remain the most universal method for assessing crocodilian distribution and relative abundance, particularly in areas where several species are sympatric. Apart from providing the benefit of immediate information on the species presence, in areas such as Taï National Park, which are affected by poaching, the presence of people performing crocodile surveys can deter illegal hunting (Campbell et al., 2011) and thus directly assist crocodilian conservation.

However, while spotlight surveys are currently the most suitable method for general crocodilian monitoring (Bayliss, 1987), surveys aiming to focus on *Mecistops* spp. should incorporate the use of playback to improve detectability, providing more accurate data on the population size and structure. Although a universal protocol for *Mecistops* spp. playback surveys is yet to be developed, broadcasting distress calls produced by hatchling and small juvenile *M. cataphractus* and *M. leptorhynchus* in their respective ranges could potentially attract the largest number of wild crocodiles. Creating a library of species-specific distress calls available for playback could ensure minimal habituation of the wild crocodiles subjected to repeated monitoring. These recordings could be obtained during crocodile captures associated with other research projects.

Despite targeting the habitat preferred and frequented by *Mecistops* in both study sites, passive acoustic monitoring did not prove to be an effective method for their detection. However, the *O. tetraspis* recordings obtained incidentally in Gabon when monitoring forest elephants (Peter Wrege, pers. comm.) suggest that passive acoustic monitoring could be employed for targeted *Osteolaemus* spp. surveys. Transects focused on *Osteolaemus* in tropical forest interior are difficult and labour-intensive, resulting in few published studies to date (Riley and Huchzermeyer, 1999; Eaton, 2010). The development of low-cost, open-source acoustic recorders (Browning et al., 2017; Whytock and Christie, 2017; Hill et al., 2018, 2019), combined with improvements and automation of the data processing (Blumstein et al., 2011; Keen et al., 2017) could provide a cheaper alternative.

Due to the lack of evidence for vocal communication recorded in the semi-natural *T. schlegelii* enclosure at Jong's Crocodile Farm, a passive acoustic monitoring trial in the wild was not deemed suitable for this species. While a playback survey was also not tested on *T. schlegelii*, the distress calls emitted by 23 wild individuals captured in Mesangat Lake, Indonesia (Staniewicz et al., 2018) did not elicit any response from conspecifics (pers. obs.). However, other emerging methods for aquatic species monitoring, such as the use of environmental DNA (eDNA), have been successful in detecting many freshwater taxa (Thomsen et al., 2012; Bohmann et al., 2014) and could be used in detecting the presence of rare crocodilians (Matt Shirley, pers. comm.) such as *T. schlegelii*.

Species detection using eDNA could also be applied to *Osteolaemus* spp. by sampling the water from streams flowing through the forest in order to obtain information on the crocodilian species present upstream from the point of sampling (Deiner et al., 2016). Areas where *Osteolaemus* is confirmed could then be monitored with a network of acoustic sensors, to obtain information on the population density and behaviour. Such system would enable non-invasive collection of long-term data. Furthermore, as information on the presence of other aquatic (through eDNA) and vocal (through passive acoustic monitoring) species is collected concurrently, the system could be used for long-term monitoring of tropical wetland communities, and their responses to habitat changes, as well as other anthropogenic pressures.

8.3 Conclusions

Crocodilians are one of the 20 most charismatic animals of the world (Albert et al., 2018), and in light of the serious threats to freshwater ecosystems, they could be used as flagships for freshwater biodiversity monitoring and conservation efforts (Carrizo et al., 2017). Opportunities therefore exist to engage NGOs, stakeholders and the general public in developing novel methods for surveying tropical biodiversity. The results I present here provide a grounding for implementing acoustic-based survey methodologies for species monitoring and conservation assessment, and suggest exciting new directions for further studies of crocodilian acoustic repertoires, behavioural ecology, and evolution.

APPENDIX A

COMPARISONS OF HABITAT FEATURES ON HANA RIVER, CÔTE D'IVOIRE

TABLE A.1. Results of the Kruskal-Wallis test comparisons of habitat features between the habitat surveys on the three segments of the Hana River: inside Taï National Park, on the park border and in the plantation area. Significant *P*-values are presented in bold.

Habitat parameter	χ^2	**df**	***P***
Percentage vegetation cover	0.338	2	0.983
Distance to shore	1.214	2	0.545
Bank slope	1.784	2	0.410
Water level	1.780	2	0.411
Distance to nearest vegetation	3.377	2	0.185
Type of the nearest vegetation	20.526	8	**0.009**

TABLE A.2. Results of the Kruskal-Wallis test comparisons of habitat feature preferences between *M. cataphractus* found in the three segments of the Hana River: inside Taï National Park, on the park border and in the plantation area.

Habitat parameter	χ^2	**df**	***P***
Percentage vegetation cover	1.233	2	0.540
Distance to shore	1.170	2	0.551
Bank slope	0.686	2	0.710
Water level	1.074	2	0.585
Distance to nearest vegetation	1.796	2	0.407
Type of the nearest vegetation	10.159	8	0.254

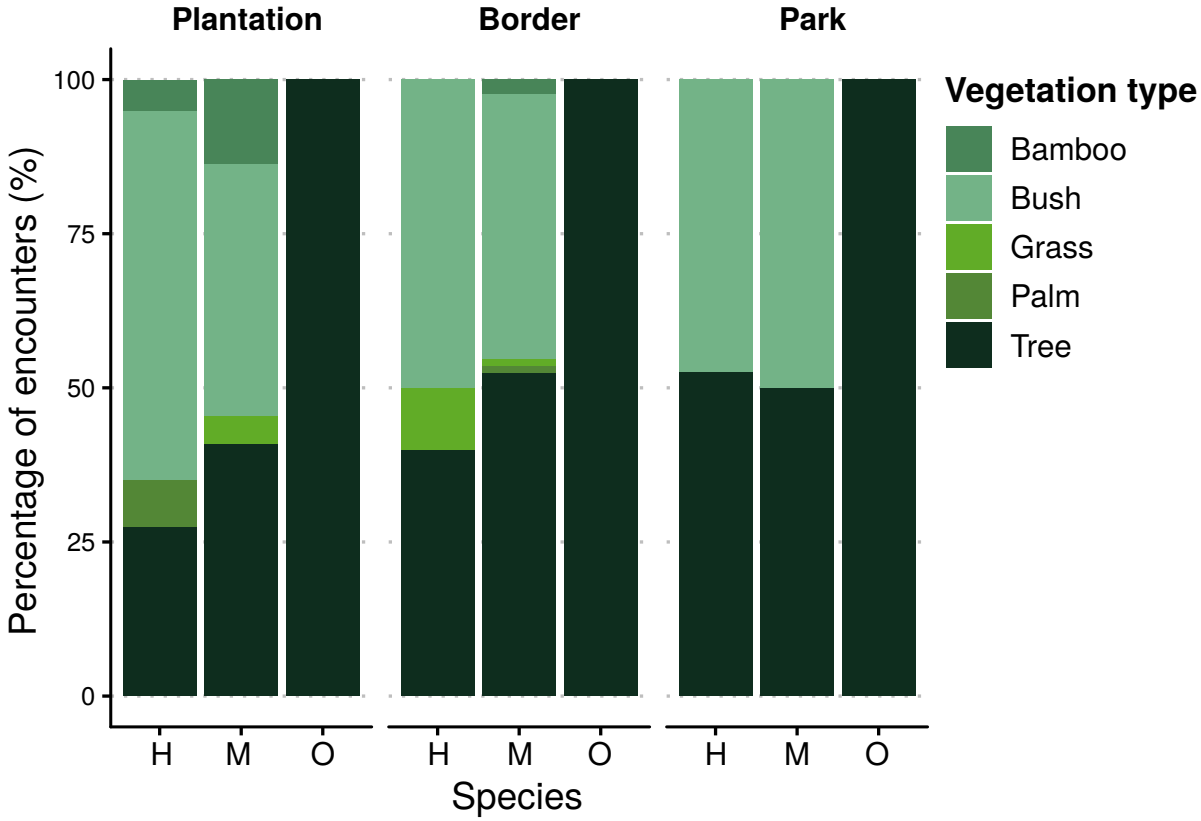

FIGURE A.1. Percentage of the nearest vegetation types to habitat survey (H, $n = 110$), *M. cataphractus* (M, $n = 125$) and *O.* aff. *tetraspis* (O, $n = 5$) location points on Hana and Meno rivers divided into plantation area, Taï National Park border and Taï National Park interior.

APPENDIX B

CONFIGURATION SETTINGS FOR THE ACOUSTIC RECORDERS IN GABON AND CÔTE D'IVOIRE

TABLE B.1. Recorder settings for the aerial (SOLO) and underwater (SM2+) recorders.

Parameter	**SOLO**	**SM2+**
Channels	1	2
Sampling rate (kHz)	8	4
Gains (dB)	31	24
Recording time	continuous	continuous
File duration (min)	10	58

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